Eesti Maaülikool
Estonian University of Life Sciences

GROUND VEGETATION DIVERSITY AND GEOBOTANICAL ANALYSIS IN THE SOUTH-WEST ESTONIAN DUNE PINE FORESTS

ALUSTAIMESTIKU MITMEKESISUS JA GEOBOTAANILINE ANALÜÜS EDELA-EESTI LUITEMÄNNIKUTES

MARI TILK

A Thesis
for applying for the degree of Doctor of Philosophy in Forestry

Väitekiri
filosoofiadoktori kraadi taotlemiseks metsanduse erialal

Tartu 2018

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to by the appropriate Roman numerals in the text. The papers are reproduced by kind permission of the publishers.

I **Tilk, M.**, Mandre, M., Klõšeiko, J., Kõresaar, P. 2011. Ground vegetation under natural stress conditions in Scots pine forests on fixed sand dunes in southwest Estonia. Journal of Forest Research, 16, 223–227.

II **Tilk, M.**, Tullus, T., Ots, K. 2017. Effect of environmental factors on the species richness, composition and community horizontal structure of vascular plants in Scots pine forests on fixed sand dunes. Silva Fennica, 51, article id 6986.

III **Tilk, M.**, Ots, K., Tullus, T. 2018. Effect of environmental variables on the composition of terrestrial bryophyte and lichen species in Scots pine forests on fixed sand dunes. Forest Systems, 27, e015.

IV Kösta, H., **Tilk, M.** 2008. Variability of bryophytes and lichens on a forested coastal dune Tõotusemägi in Southwestern Estonia. Forestry Studies, 49, 71–80.

The contributions of the authors to the papers were as follows:

	I	II	III	IV
Original idea	MM, **MT**	**MT**	**MT**	HK, **MT,** MM
Study design	MM, **MT**	**MT**	**MT**	HK, **MT**
Data collection	**MT**, JK, PK	**MT**	**MT**	HK, **MT**
Data analysis	MM, **MT**, JK	**MT**, TT, KO	**MT**, TT, KO	HK
Preparation of the manuscript	MM, **MT**	**MT**, TT, KO	**MT**, TT, KO	HK, **MT**

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ABBREVIATIONS

N_{total}	Content of total nitrogen
P	Content of phosphorus
Ca	Content of calcium
K	Content of potassium
Mg	Content of magnesium
VWC	Volumetric soil water content
ISA	Indicator species analysis
MRPP	Multi-response permutation procedures
NMDS	Non-metric multidimensional scaling
S	Species richness
S_{vasc}	Vascular plant species richness
S_{bryo}	Bryophyte species richness
S_{lich}	Lichen species richness
D'	Simpson's diversity index
K_k	Koch index for biological homogeneity
K_s	Sørensen's similarity coefficient
EC	Soil-water solution electrical conductivity
PAR	Photosynthetically active radiation
pH	Soil-water solution hydrogen ion concentration
CC	Canopy cover

1. INTRODUCTION

Sand dunes occur in different shapes in deserts and coastal areas worldwide (Herrmann *et al.* 2008). Dune habitats are characterised by high ecological diversity. The wooded dunes of the Boreal region are recognised as being one of Europe's priority habitats (Council of the European Union 1992). Baltic coniferous coastal dune woodlands are listed as vulnerable habitats in the European Red List of Habitats (European Commission 2016).

Latvian, Lithuanian and Estonian western seacoasts are characterised by sand dunes of various ages with complex and fragile habitats. Human activity is one of the main factors besides climate warming and atmospheric nitrogen deposition altering coastal habitats (Kutiel *et al*. 2000; Grunewald 2006; Bobbink *et al*. 2010). Wooded dunes are considered to be especially sensitive to trampling and vehicular traffic, which results in the deterioration of vegetation (Burden & Randerson 1972; Örd 2000).

Vegetation is reckoned to be key to dune stability (Provoost *et al*. 2011). Biodiversity is considered to be the foundation of ecosystem services, and thus its preservation has worldwide importance (Sala *et al*. 2000; Conference of the Parties 2010; Piaggio *et al*. 2017). Clarification of the environmental factors that determine ground vegetation species richness and species composition in forested inland dunes is vital in order to adequately plan and enforce conservation of these habitats.

The current thesis focuses on the ground vegetation (vascular plants, bryophytes and lichens) of forested dunes of various heights in south-west Estonia, in order to determine the environmental factors that shape ground vegetation communities in these dry and nutrient-poor habitats. Research gives new data on the variation of site conditions and ground vegetation biodiversity on inland forested dunes. For this purpose, the following aspects were studied: environmental factors that affect vascular plant species richness, species composition and horizontal structure (**I**, **II**); environmental factors that influence terrestrial bryophyte and lichen species composition on forested dunes (**III**; **IV**); and ground vegetation zonation on dunes of various heights (**I–IV**, current thesis).

2. REVIEW OF THE LITERATURE

The maintenance of biodiversity is an integral part of sustainable forest management and a desirable goal for most forest-related initiatives and legislative bodies. Assessments of biological diversity are essential for understanding forest ecology, while monitoring sustainable forest management binds conservation to the enhancement of biological diversity (MCPFE Liaison Unit Vienna 2002; Canullo *et al*. 2013).

The majority of plant biodiversity in a Boreal zone forest ecosystem is concentrated in the ground vegetation layer, which accounts for more than 80% on average of the total plant species richness of a forest (Alberdi *et al*. 2010). Ground vegetation is usually defined as a forest layer consisting of all vascular plant species of up to one metre in height; variations in definitions are the result of differences in height distinction and the inclusion or exclusion of non-vascular plant species such as bryophytes (Gilliam 2007).

Geobotany, also called phytogeography or phytocenology, is the study of plants and their geographical distribution (Blydenstein 1961; Collin 1992) in which the essential goal is to determine reasons for the spatial distribution of species (Rübel 1927). One of the first geobotanists to divide Estonian territory according to relief and plant formations was J.G. Granö, who in 1922 identified fifteen categories. Teodor Lippmaa, one of the most influential geobotanists in Estonia (Lippmaa 1933, 1935, 1938), divided Estonia into four districts — the islands and coastal district, the Silurian district, the Subsilurian district and the Devonian district — along with nine categories. Subsequently, Liivia-Maria Laasimer (1958) divided Estonia into two districts — the East-Baltic district and the West-Baltic district — and eight divisions. The Teodor Lippmaa approach is also called the synusiae approach; a synusia is an elemental vegetation unit defined as a set of plants of one layer with the same ecological condition requirements (Trass 1965, 1976). Acknowledging the relations of different site condition to species richness patterns is crucial before drawing any conclusions on the effects of biodiversity on ecosystem processes (Pausas & Austin 2001; Hart & Chen 2006).

Plant ecologists explore variable environmental factors to clarify ground vegetation species distribution and diversity; climatic factors such as temperature and light, soil water content, plant-available nutrients, carbon balance, heterogeneity of microsites and disturbance regimes are believed to be the primary factors controlling ecosystem processes and species distribution (Stephenson 1990; Neilson 1995; Roo-Zielinska & Solon 1997; Beatty 2003; Bartels & Chen 2010; Alatalo *et al*. 2015; Del Vecchio *et al*. 2015; Márialigeti *et al*. 2016). The ability of vascular plant cover to respond to changes in environmental factors relatively rapidly makes it an easily identifiable and recognisable characteristic of the natural environment (Solon *et al*. 2007).

2.1 Wooded dunes

The wooded dunes of the Boreal region are a priority habitat according to the Council of the European Union (1992). Wooded dunes are classified as natural or semi-natural long-established dunes with a well-developed woodland structure (European Commission 2013). In Europe, wooded dunes are primarily seen as being the sea dunes of the Atlantic, the North Sea, Baltic coasts and the Mediterranean coast. Although Estonia is a small country, it has a long coastline (approximately 3,800 km) along the Baltic Sea. Its largest dune habitats are situated on the west-facing coast (Doody 2017). According to the European Red List of Habitats, the wooded dunes in the Rannametsa area belong to the Baltic coniferous forests (B1.7d) coastal habitat type (European Commission 2016); according to T. Lippmaa's (1935) geobotanical classification, the Rannametsa dune system belongs to the islands and coastal area district (districtus litoralis), coastal area category (Estonia litoralis) and Häädemeeste subcategory (litorale hedemeesteense); and according to L.-M. Laasimer (1958), it belongs to the West-Baltic geobotanical district, the West-Estonian mainland and islands meadows and wooded meadows division, and the mainland western part dry meadows and wooded meadows subdivision.

The Rannametsa dune system is one of the most representative dune areas of Estonia and consists of two dune ridges: the landward dune ridge of the Ancylus lake (height up to 10 m) and the seaward dune ridge of the Litorina Sea (height over 20 m) (Ratas & Rivis 2003). Some of the dune *Pinus sylvestris* L. forests, including the dune area from Häädemeeste to Uulu, have been under some kind of protection for centuries (Örd 2000) because of their fragile nature and complex conditions for recovery. The first records of attempts to protect dune forests date back to 1786, when the governors accepted laws to protect old forests in the Rannametsa, Häädemeeste and Uulu areas (Kose *et al*. 2003). According to legislative acts from 1839 and 1888, dune forests were viewed as surface protection forests (Meikar 2001). The harvesting of single trees, picking up of dead wood and branches or collection of litter or lichens-bryophytes were all forbidden (Kose *et al*. 2003; Meikar 2014). The protected dune forests were mostly owned by state manors: Tahkuranna (Tackerort) and Häädemeeste (Gudmannsbach) (Tammekann *et al*. 1930). In 1958 the dunes between Võiste and Häädemeeste gained the status of a Nature Conservation Area and in 1964 the Rannametsa dunes were established as a Landscape Protection Area (Kose *et al*. 2003). In 1991, the area was named the Rannametsa-Soometsa Landscape Reserve (Kose *et al*. 2003). The Luitemaa Nature Reserve was established in 2000 and a further area added in 2004. According to the Estonian Nature Information Centre, nowadays the area of the Luitemaa Nature Reserve is 11,301 hectares (LPMP 2017). The dune forest area near Uulu was designated the Uulu-Võiste Protection Area in 2007 and subsequently renamed the Uulu-Võiste Landscape Protection Area, with a size of 687 ha, in 2017 (UPMP 2016).

Dry coastal ecosystems have been in researchers' spotlights from the early days of ecology as a science (Van Der Maarel 2003), dune succession, vegetation, soil conditions and ecology being the main topics of interest (Cowles 1899; Snow 1902; Watson 1918; Richards 1929). In Estonia, the dunes have been thoroughly investigated: their formation, history and geology, by Orviku (1933), Eltermann and Raukas (1966), Raukas (1968) and Kose *et al*. (2003); their soils in the south-west, by Örd (1972a, 1972b) and Ratas and Rivis (2003); and aspects of their vegetation and forestry, by Ilves (1966), Örd (1973), Mandre (2000; 2003), Pärn (2003), Klõšeiko (2003), Mandre and Ots (2003) and Mandre *et al*. (2006). The recreational value of dunes and aspects of forestry have been discussed in considerable depth by Örd (1972a) in his candidate dissertation. Nevertheless, although many aspects of the dunes have been thoroughly investigated, the main focus has been on coastal dune systems while already formed ecosystems on inland dunes have received less attention so far. Therefore, valuable complex and statistically relevant information about fine-scale variations in ground vegetation communities and their relationships to environmental factors on forested inland dunes is still lacking. Although the effects of topography have been investigated with reference to large-scale landforms, the general importance of topography is less recognised and mechanisms by which it exerts effects on local plant diversity still stays unclear (Moeslund *et al*. 2013). Pausas and Austin (2001) suggest to study multidimensional gradients of resources and environmental parameters using non-linear regression techniques and interactions because non-linear patterns are too common in nature to be omitted in the analysis of species richness.

According to the Hutchinsonian niche theory (Hutchinson 1957), there is a positive relationship between species richness and habitat heterogeneity. Fixed dune landscapes are acknowledged to be specific landforms with specific topographical features and many variations in aspect, slope angle and micro-climate (Houston 2008; Mandre *et al*. 2008). Soil conditions, and even forest site types, can differ drastically between slopes (such as *Cladonia*, *Calluna*, *Rhodococcum* and *Myrtillus* forest site types) (Raukas 1968; Chandapillai 1970; Örd 1972a; Mandre & Korsjukov 2003).

On the basis of their literature review, Bartels and Chen (2010) argued that the species diversity of a forest ecosystem is dependent on the developmental stage of resource quantities, but that after maturing species diversity is more affected by resource heterogeneity. Drawing on various studies, Pausas and Austin (2001) concluded that species richness increases with temperature and water availability as well as greater environmental heterogeneity. Huston (1979) found fine-scale species richness to be driven by two universal key factors — disturbance and a decrease in productivity — while Nylén and Luoto (2015) added the successional stage of a dune to this list of factors. According to Peyrat (2007), an increase in soil organic matter and therefore soil nitrogen can be observed with increasing vegetation cover. In his study, Lichter (1998) found species richness to change unimodally with increasing dune age and along gradients of soil moisture and soil N, Ca and Mg content on the coniferous dune forests of northern lower Michigan. Soil P, on the other hand, showed an increase with increasing species richness at earlier stages of succession but a decrease with decreasing species richness at the climactic succession stage (Lichter 1998).

2.2 Environmental factors on inland dunes

Geographic vegetation zonation has been used to characterise the development of vegetation on dunes at varying fixation and succession stages (from the beach to the forest) in numerous studies (Johnson 1982; Hundt 1985; Isermann 2011; Ciccarelli 2015). Less attention has been paid to the smaller-scale zonation of ground vegetation on dune slopes and the factors causing it. Site factors can be divided into external and internal factors: external factors are not part of the forest ecosystem and are considered to be independent of each other, while internal factors belong to the forest ecosystem and develop through mutual influences (Jenny 1980; Elgersma 1998).

The successional age of dunes affects their species diversity patterns (Isermann 2011). Compared with succession traits in coastal sand dunes, successional pathways on inland dunes occur quite uniformly (Ujházy *et al*. 2011). The succession of Boreal dunes moves towards pine forests; it takes nearly 300 years for a forest ecosystem to develop on dunes (Lichter 1998). On the inland dunes studied by Ujházy *et al*. (2011) in the Netherlands, the pine forest's herb layer was commonly dominated by *Deschampsia flexuosa* (L.) Trin. Some differentiation appears to be related to site moisture and relief type: *Empetrum nigrum* L.

subsp. *nigrum* is found on relatively moist dune plateaus and the northern slopes of dunes, while *Vaccinium myrtillus* L. prefers mesic sites and *Vaccinium vitis-idaea* L. is common in dry areas (Ujházy *et al*. 2011). The presence of lichens appears to be related to the successional age of dunes (Ketner-Oostra & Sykora 2000). Terrestrial lichens are mainly acidophytic (Gheza *et al*. 2015) and lichen species composition is significantly related to soil acidity; lichen-rich communities are restricted to soils with a pH_{H2O} of 5.7—6.3 (Ketner-Oostra & Sykora 2000) in which cryptogams are better competitors than are herbs (Ahti & Oksanen 1990; Isermann 2011; Jüriado *et al*. 2016). Although dune forests are the final stage of dune succession, turnover of ground vegetation species still occurs during that time. Vegetation succession and soil development during ageing increases carbon and nitrogen percentages in dune soil and soil acidification, causing a shift from lichen-rich stands to moss-dominated stands (Ketner-Oostra & Sykora 2000).

Soil patterns in coastal dunes are very complex and topography is one of the decisive factors for soil formation processes, affecting the variability and distribution of ground vegetation (Jenny 1941; Zoladeski 1991; Peyrat 2011; Soil Science Division Staff 2017). Differences in the properties of soils and microclimates are related to the slope aspect of the dunes (Sewerniak & Jankowski 2015). According to Eltermann and Raukas (1966), the Rannametsa dune relief is atypical: in the Rannametsa area, the seaward and landward slopes of the dunes are both relatively steep (25—45 degrees) and are therefore peculiar landforms that can affect ground vegetation patterns. Soils on dunes have been considered areas of rather monotonous soil cover (Elgersma 1998), but Sewerniak *et al*. (2011) found that soils on north-facing slopes are characterised by higher pools of total organic carbon, nutrients and soil moisture. Southern slopes, on the other hand, are more exposed to solar radiation and are described by higher soil temperature and lower soil moisture (Maun 2009; Sewerniak *et al*. 2017).

Topographically-induced changes are found for soil nutrients; e.g. northern slopes are characterised as being more fertile (Sigua *et al*. 2011; Sewerniak *et al*. 2017). Changes in nutrient supply affect the species composition and the competition between plant species in dune plant communities (Lane *et al*. 2008). The chemical and physical characteristics of soil in the rooting zone, which is up to 20 cm for the majority of vascular plant species, are important in shaping the vegetation structure (Bednarek *et al*. 2005). Soil electrical conductivity is considered to be one of the simplest, cost effective soil measurement techniques to assess the variability of soil salinity (Chan *et al*. 2006). Coastal soils can be enriched with water-soluble salts (Corwin & Lesch 2005), which may have detrimental effect on soil chemical and physical properties (Leone *et al*. 2007). In addition, soluble salts lower the osmotic potential of the soil water, thus, a lower plant leaf water potential is required to sustain transpiration (Leone *et al*. 2000; Brady & Weil 2002).

The results of Solon *et al.* (2007) showed that the sequence of changes in soil characteristics is reflected in the sequence of changes in plant communities. During succession, nutrient mineralisation takes place and organic matter accumulates; this drastically decreases the soil pH and Ca-ion content, which in turn causes species turnover over time (Berendse 1998). Weathering processes and rainfall cause a rapid, leaching loss of calcium during dune succession and decalcification is usually accompanied with the acidification of soils (Peyrat 2007). Airborne pollutants are recognised as a major threat to Baltic coastal dunes (Remke *et al*. 2009; Peyrat 2011). Atmospheric nitrogen deposition has negative impact on ground vegetation species richness (Provoost *et al*. 2011; Kooijman *et al*. 2017). Higher nitrogen deposition causes grass encroachment and changes in species composition, especially the decrease of characteristic herbs (Kooijman *et al*. 1998; Kooijman *et al*. 2017). It has been found that in acidic coastal dunes of the Baltic Sea, the critical load has been estimated up to 4 kg N ha^{-1} yr^{-1} wet deposition or total of 5—8 kg N ha^{-1} yr^{-1} (Remke *et al*. 2009).

Although soils on fixed forested dunes are usually acidic Podzols, soil type can change throughout the dune's profile (Õrd 1972a, 1972b; Mandre *et al*. 2006; Peyrat 2007; Mandre *et al*. 2008; Sewerniak *et al*. 2017). According to Peyrat (2007), Haplic Podzols can be found under undisturbed dune forests; the climax of soil formation was reached in the Podzol stage beneath a 160-year-old pine forest at the Russian part of the Curonian Spit near the Baltic Sea; also the amount of acidic mor-type humus increases with plant cover. Lateral podsolization in Poland has been verified by Jankowski (2014), who found evidence of slope-scale element translocation. In the Netherlands, organic matter is thought to be the primary source of nutrients in nutrient-poor sandy soils (Elgersma 1998) and to have an impact on soil moisture conditions (van Mierlo *et al*. 2000). Sewerniak *et al.* (2017) found that soils on inland dunes differ in the thickness of the O-horizon, with the highest values being recorded on northern slopes. Primitive sandy soils have a thin humus horizon which on dunes is commonly found at the bottom but is absent from their slopes and tops (Mandre *et al*. 2008), thus modifying their soil water-holding capacity (Elgersma 1998).

Dune areas are known as dry ecosystems with a very low water-retaining capacity (Chandapillai 1970; Van der Maarel 1993). Fixed sand dunes are so dry that they inhibit the physiological processes of plants (Niu *et al*. 2005). Soil moisture appears to increase through the accumulation of soil organic matter (Berendse 1998). Spatial variation in soil moisture in turn creates a broad range of habitats in which different species can co-exist (Sack & Grubb 2002). According to Ensign *et al*. (2006), in a sand dune system in a temperate-humid region the presence and type of vegetation has more influence on soil moisture than does topography.

Grey dunes (i.e. dunes stabilised by herbaceous vegetation) and brown dunes (i.e. dune heath), as well as dune forests, have moderately or even highly acidic soils (Örd 1972a; Isermann 2005). Soil pH in dune areas is variable and, according to Isermann (2005), can vary by up to nearly a full unit in samples separated by 1 metre. According to Grime (1973), species richness reaches its maximum when soil pH is 6.1—6.5, the number of species dropping when the pH goes any higher or lower. Soil acidity and moisture are very important factors for explaining species richness patterns (Schaffers 2002) and large pH variability is likely to be caused by the vegetation structure (Isermann 2005). Solon *et al.* (2007) found that the soil pH and soil moisture interaction influences species richness negatively in cases both where soil moisture and pH are high and where soil pH is lower but moisture is higher.

Light conditions on forested dunes are related to the stage of stand development. Understorey light conditions are considered to be one of the most important factors influencing the growth and development of vegetation beneath a forest canopy (Lieffers *et al*. 1999). Ground vegetation development, diversity and structure are highly limited by light availability (Bartels & Chen 2010). The amount of light that penetrates through canopy depends on the size, distribution and density of tree crowns (Brunner 1998). Solar radiation availability for ground vegetation is also greatly affected by topography, through slope orientation and the presence of other topographical obstructions (Zou *et al*. 2007). Light availability is an extremely variable factor that depends on stand heterogeneity (Härdtle *et al*. 2003). Because of dune topography, north-facing slopes receives less solar radiation than south-facing slopes do (Sewerniak 2016); lichen-dominated patches (*Cladonia* P. Browne spp.) are characteristic of sunny southern slopes, whereas bryophytes (e.g. *Pleurozium schreberi* (Brid.) Mitt.) usually dominate northern slopes (Oksanen 1983).

Numerous hypotheses with different views try to explain species diversity patterns. According to the Intermediate Disturbance Hypothesis (Connell 1978), the highest species richness occurs at intermediate levels of environmental resources and disturbance gradients; naturally stressed dune areas are extremely fragile ecosystems. According to biodiversity-stability theory (MacArthur 1955), the highest stability of an ecosystem occurs with the highest biodiversity. To protect these areas, we must protect their biodiversity. Current assessments of dune habitats show their poor conservation status in Europe (European Commission 2015). According to the European Red List of Habitats report, Baltic coniferous coastal dune woodlands have been assessed as being a vulnerable habitat group (European Commission 2016). Acknowledging the rising recreational pressure placed on such areas all over the world, further action and research should be implemented. The vision of the Strategic

Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets is as follows: 'By 2050, biodiversity is valued, conserved, restored and wisely used, maintaining ecosystem services, sustaining a healthy planet and delivering benefits essential for all people'. It is recognised by 196 parties and has been signed by 168 countries (Conference of the Parties 2010). Thus, research on dune habitats is especially important today.

3. AIMS AND HYPOTHESES OF THE STUDY

Aims of the thesis:

- To determine and analyse which site- and canopy-related factors affect the ground vegetation diversity and species composition of *Pinus sylvestris*-dominated forest ecosystems on dunes (**I**; **II**; **III**).

- To detect whether a sequence of changes in site topographical and environmental factors is reflected in a sequence of changes in the species composition of ground vegetation (zonation) (**I–IV**).

- To provide new knowledge concerning the vascular plant species richness and composition of ground vegetation in *Pinus sylvestris* forests on fixed sand dunes (**I**; **II**).

- To analyse the variability of bryophyte and lichen communities and species distribution patterns in *Pinus sylvestris* forests on fixed sand dunes (**III**; **IV**).

The main hypotheses of the study:

- On dunes, ground vegetation changes are in accordance with changes in dune topographical and environmental factors and clear vegetation patterns are distinguished between zones — bottoms, slopes and tops of the dunes, and ground vegetation zonation is more visible on higher dunes than on lower dunes (**I–IV**).

- Vascular plant species composition and richness of ground vegetation are affected by differences in the properties of soil and light conditions on the dunes (**I**; **II**), while higher soil nitrogen content reduces vascular plant species richness (**II**).

- Bryophyte and lichen species composition is significantly influenced by edaphic factors like soil moisture regime and soil pH; lichen species richness increases in areas with a lower vascular plant species cover (**III**; **IV**).

4. MATERIAL AND METHODS

4.1 Study area

To investigate the ecosystems on dunes, five typical dunes were selected in the coastal area of the Baltic Sea in south-west Estonia (Figure 1) (**I**; **II**; **III**; **IV**). The average distance of the study sites from the Baltic Sea coast is approximately 2—3 km.

Sites No. 1, 2 and 5 are located in the Luitemaa nature reserve, where fixed coastal dunes with herbaceous vegetation (grey dunes) (type 2130*), wooded dunes of the Atlantic, Continental and Boreal region (type 2180) and humid dune slacks (2190) are under protection (Council of the European Union 1992). Site No. 5 was used as a pilot area to test the research methodology. Sites No. 3 and 4 are situated in the Uulu-Võiste landscape protection area, where three priority habitats according to the Council Directive 92/43/EEC are present: the wooded dunes of the Atlantic, Continental and Boreal region (type 2180), the Western Taïga (type 9010*) and Fennoscandian deciduous swamp woods (type 9080*).

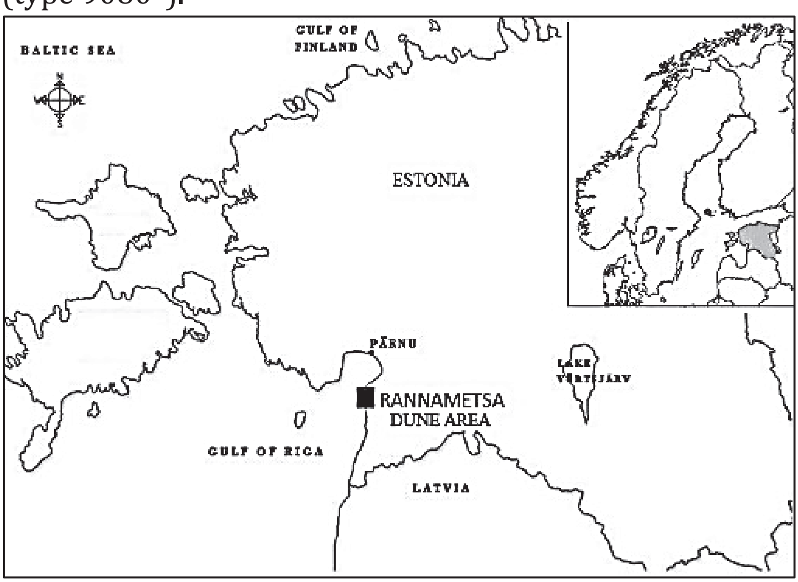

Figure 1. Location of the study area and study sites.

Precise locations and heights of the sites were measured with Garmin GPSMap 76CSx. The height of the dunes varies between 12 and 33 m (Table 1). Average stand descriptive characteristics for the dunes studied were received from the State Forest Management Centre database for the quarter in which the dune is located and are presented in Table 1.

Table 1. Average characteristics of investigated dunes and stands.

Dune	Site 1	Site 2	Site 3	Site 4	Site 5
Loc	58°8´20″N 24°30´27″E	58°8´23″N 24°30´36″E	58°14´28″N 24°31´21″E	58°13´51″N 24°30´47″E	58°7´56″N 24°30´36″E
H_{abs}	28	33	12	10	32
H_{rel}	16	21	6	6	20
C_{stand}	0.45	0.54	0.62	0.60	0.39
Age	180	190	200	210	200
H_{stand}	24	24	21	23	25
Q_{index}	IV	IV	IV	IV	III
D_{und}	Low	Low	Low	Low	Low
Papers	**II**; **III**	**II**; **III**	**II**; **III**	**I**; **II**; **III**	**I**; **IV**

Loc – location of dune; H_{abs} – absolute height of dune, m; H_{rel} – relative height of dune, m; C_{stand} – stand cover index; Age – stand average age, yr; H_{stand} – average height of stand, m; Q_{index} – site quality index; D_{und} – density of tree layer understorey.

The forests in the study area are mostly single-species pine stands, most of which (83.8%) are of natural origin (Pärn 2003). Study sites were selected in areas with single-species pine stands. In 2003, middle-aged stands were predominant, although a large quantity of overmatured stands was also found (Pärn 2003). According to Mandre and Korsjukov (2003), forest site type varies along the dune profile: *Vaccinium myrtillus* forest site type is found at the bottom, *Rhodococcum* forest site type on the slopes and *Cladonia* and *Calluna* forest site types on the higher parts of the dune profile. Similar results were observed by Örd (1972a). Pärn (2003) found 16 forest site types in single-species pine stands, the most common being *Cladonia*, *Rhodococcum* and *Myrtillus*. Based on the results of Kõresaar *et al*. (2008) for the *Rhodococcum* forest site type on the old pine stand in the Rannametsa-Uulu area, the average Orlov quality class was III, the relative density 0.56 and the shelter 0.37. The same characteristics were estimated for the *Cladonia* forest site type: Orlov quality class III, the relative density 0.63 and shelter 0.53 (Kõresaar *et al*. 2008).

4.2 Climate

The main climatic characteristics during the study periods, according to the closest weather station of the Estonian Meteorological and Hydrological Institute in Pärnu, are presented in Table 2.

Table 2. Average climatic characteristics during different study periods (Estonian Meteorological Institute database).

Year of the field studies	2004 (**IV**)	2006 (**I**)	2008 (**I**; **II**; **III**)	2010 (**II**; **III**)	2016 (**II**; **III**)
Annual temperature	6.6 °C	7.4 °C	7.6 °C	5 °C	6.8 °C
Average minimum	-6.5 °C (Jan.)	-9.4 °C (Feb.)	-0.6 °C (Jan.)	-12.3 °C (Jan.)	-7.7 °C (Jan.)
Average maximum	17.4 °C (Jul., Aug.)	18 °C (Aug.)	16.6 °C (Jul.)	21.8 °C (Jul.)	17.8 °C (Jul.)
Total precipitation	760.6 mm	573.9 mm	861.5 mm	908.4 mm	673.2 mm
Average minimum	8.3 mm (Apr.)	11.6 (Jan.)	17 mm (May)	27 mm (Jan.)	23.3 mm (Dec.)
Average maximum	116.5 (Jun.)	108.2 (Oct.)	147.5 mm (Aug.)	122.8 mm (Aug.)	141.9 mm (Aug.)
Relative air humidity	80%	80%	83%	84%	82%
Length of growing period	214 days	192 days	232 days	203 days	189 days
Permanent snow cover	86 days	106 days	0 days	112 days	32 days
Days with snow	99 days	125 days	48 days	143 days	83 days

4.3 Data collection

4.3.1 Environmental factors

Topographical factors

In 2007, the absolute altitudes (H_{abs}, m.a.s.l) and cardinal directions of the transects were measured using a Garmin GPSMap 76CSx device, while relative height (H_{rel}, m) was calculated taking the first quadrat of the transect as zero (Table 1) (**I**; **II**; **III**).

Quadrat angles were assessed using an inclinometer for every quadrat and classified into five classes: 1 (1—10 degrees); 2 (11—20 degrees); 3 (21—30 degrees); 4 (31—40 degrees) and 5 (41—50 degrees) (**II**; **III**). Based on the angle classes, sites No. 1, 2 and 5 are referred to as higher dunes (slope angles reach angle classes 3—5) and sites No. 3 and 4 as lower dunes (slope angles belong to angle classes 1 or 2).

Soil horizons

In 2004 and 2007, on sites No. 4 and 5 the soil horizons on western slopes were described to the depth of 1 m from the surface and the thicknesses of the different horizons measured based on Owens & Rutledge 2005 (**I**).

To give more precise information about soil conditions and soil types according to the cardinal direction of the slopes, in 2016 soil pits were dug and different soil horizons: organic horizon (O), humus horizon (A), eluviated horizon (E) and peat horizon (T) thicknesses up to 20 cm were measured across the dunes on the bottoms, slopes and tops (in each zone n=3) at the transects on sites 1, 2, 3 and 4. Soil organic horizon (O-horizon) thickness and its decomposition rates were categorised as follows: O1 (Oi) — poorly decomposed sub-horizon; O2 (Oe) — moderately decomposed sub-horizon; and O3 (Oa) — well decomposed sub-horizon.

All soil types were classified according to the Estonian soil classification system (Astover *et al*. 2012) and named after the internationally recognised World Reference Base for Soils (WRB) classification (FAO 2015) (**II**; **III**).

Soil pH and electrical conductivity

In 2004, to assess soil pH in different zones on the line transect (**IV**) three randomly chosen sample points were established for collecting soil samples from the upper 2 cm soil organic layer in every zone (n=36). The pH was measured in the laboratory of the Estonian University of Life Sciences, Forest Research Institute, Department of Ecophysiology and determined (n=5) in a soil-water suspension (1:5) using a Mettler Toledo MP220 laboratory pH-meter.

To test for pH and electrical conductivity, composite soil samples to a depth of 20 cm were collected from every quadrat on sites 1, 2, 3 and 4 (n=232) in July 2010 (**I**; **II**; **III**). Before collecting the composite soil sample, the poorly decomposed litter layer was removed. Electrical conductivity (EC, $\mu S\ cm^{-1}$) is the measurement of electrolytes in a solution, EC has been used commonly in agriculture to map the spatial variation of the salt content of the soil (Corwin & Lesch 2005; FAO 2006). The electrical conductivity of soil can be viewed as an indirect measurement that correlates with several physical and chemical soil properties.

Soil pH and electrical conductivity were measured from a soil-distilled water mixture (1:2.5 or 1:5 for samples with high organic matter content) using a Eutech Instruments PC300 pH/conductivity meter with automatic temperature correction.

Soil nutrients

In order to describe and assess the soil conditions for ground vegetation, it is important to collect soil samples from the main root zone of ground vegetation (Härdtle *et al*. 2003). The majority of the rooting zone for most vascular plants is found at a depth of

20 cm (Bednarek *et al*. 2005; Solon *et al*. 2007), the depth also recommended by the FAO (2006).

In 2004 and 2007, soil pits were dug to collect soil samples from the bottoms, slopes and tops (n=3 per zone) of the western slopes on sites No. 4 and 5 and composite samples from mineral topsoil (up to 30 cm) were analysed for total content of N (N_{total}) and contents of plant-available P, K, Ca and Mg (**I**).

To describe variability in growth conditions over the dune profile and at different cardinal directions, soil samples from mineral topsoil for analysing N_{total}, P, K, Ca and Mg levels were collected in May 2016 at a depth of 20 cm (n=3 per zone) on the bottoms, slopes and tops of the dunes at sites 1, 2, 3 and 4 (**II**; **III**).

The contents of N_{total}, P, K, Ca and Mg available to plants were determined from composite samples in the Laboratory of Agrochemistry of the Estonian Agricultural Research Centre (**I**) and in the Laboratory of Plant Biochemistry of the Estonian University of Life Sciences (**I**; **II**; **III**); P and K were determined by the ammonium lactate method, Ca and Mg by the ammonium acetate method and N_{total} by the Kjeldahl method (**I; II; III**).

Soil moisture conditions

Volumetric water content (VWC, %) was used as a numerical measure of soil moisture to estimate the amount of stored water in the soil. It was determined for every quadrat using Field Scout™ TDR 300 at a depth of 20 cm (n=3).

Time-domain reflectometry (TDR) is a technology that quickly and accurately determines volumetric water content in soil by measuring the travel time of an electromagnetic wave along a waveguide (more specific information is available from Spectrum Technologies, Inc.). The meter converts the measured electrical signal into a percentage of soil moisture using an equation that is valid for a wide range of mineral soils. This data was collected in May, July and September 2008, with the precondition that no rain had fallen for at least three days before measurement (**I**; **II**; **III**).

Light conditions

In every quadrat on sites No. 1, 2, 3 and 4, two evaluators visually assessed canopy cover as a measure of the percentage of forest floor covered by the vertical projection of tree canopies expressed on a scale of 0 to 1 (Masing 1979; Pihelgas 1983). The fraction of below-canopy photosynthetically active radiation (PAR) was measured using the Decagon Devices AccuPAR (Model PAR-80) light-interception device. The measurements were performed on all sites on 23 July 2008, during a very short time period on a clear, sunny midday (**II**; **III**). The probe of the AccuPAR light-interception device contains 80 independent sensors, spaced 1 cm apart, which measure PAR in the 400 to 700 nm waveband. The probe was placed at heights above ground vegetation parallel to the ground. The spatial variance of below-canopy light conditions is considered to be large, therefore a large number of below-canopy samples was obtained (n=10 readings per quadrat; in all 2,320 measurements as well as averages of the readings per quadrat were taken electronically using this ceptometer).

4.3.2 Ground vegetation

To study the ground vegetation, quadrats of 1 m^2 in size and forming a continuous line transect over the dunes were established. The transect started from the bottom of the dune, moving over the top to the bottom at the other side with quadrats located at 1 m intervals along line transect, except on site No. 5 where only the western slope of the dune was included.

On site No. 1, the transect started from the southern bottom of the dune and moved continuously over the dune top to the northern bottom. Here, 58 quadrats were analysed in total. On the highest dune, dune No. 2, there were 108 quadrats on the transect from west to east. On site No. 3, the transect covered 32 quadrats from south to north, while on dune No. 4 a transect of 34 quadrats ran from west to east. Finally, 19 quadrats were analysed on the western side of site No. 5.

In all the quadrats, total cover of the vascular plant species, bryophyte and lichen layers as well the cover of each species separately were estimated visually on a scale of 1–100%. Dominant species were determined based on abundance (Braun-Blanquet five-point scale) (**I**; **II**; **III**).

The research presented in papers **I** and **IV** were pilot studies to test methodology.

Vascular plant species

Descriptions of vascular plant communities were provided for the quadrats of continuous line transects in July 2006 (**I**) on the western slope of the Site No. 5, and for the transects on sites 1, 2, 3 and 4 in May, July and September 2008 (**I**, **II**), to take into account seasonal features of the vegetation and record total species composition.

For each of the quadrats vascular plant species composition was determined (Kalda 1966; Masing 1979), the nomenclature used following the keybook of Estonian vascular plants (Leht 1999) (**I**; **II**).

Lichens and bryophytes

Field studies of bryophytes and lichens were carried out in 2004 and 2010. In June 2004, lichens and bryophytes were determined on site No. 5's western slope (**IV**). The line transects began at the bottom and moved toward the top of the dune, resulting in a transect length of 183 metres. Bryophyte and lichen species were identified one metre on either side of the transect. On the transect, bryophytes and lichens were collected from different substrates (ground, tree trunks, stumps, litter).

In July 2010, bryophyte and lichen determination was carried out in the same quadrats as those used for the vascular plant species investigation on sites No. 1, 2, 3 and 4 in 2008 (**III**). Additional quadrats (n=464) were formed 1 m to the left and 1 m to the right of the basic quadrat and the species not occurring in the basic quadrat determined.

Lichen species were determined according to the Estonian Keybook of Macrolichens (Trass & Randlane 1994), bryophytes with the Keybook of Estonian Bryophytes (Ingerpuu *et al*. 1998) (**III**; **IV**). Any samples not identified in the field were collected and determined in the laboratory.

For the identification of lichens, three different reagents were used: 10% KOH hydrosol, $Na(ClO)_2$ saturated hydrosol and 5% $C_6H_4(NH_2)_2$ alcoholic solution. Using these reagents on the cortex, medulla or apothecia of lichen thallus causes colour reactions that reveal the existence or absence of different lichen substances in the samples (**III**; **IV**).

To identify bryophyte and lichen species, use was also made of the Tallinn Botanical Garden's bryophyte and lichen herbarium for comparison analysis, as well as Tallinn University and Tallinn Botanic Garden's dissecting and compound microscopes (**III**; **IV**). Consultations also took place with lichen specialists at the University of Tartu and a bryophyte specialist at Tallinn Botanic Garden (**III**).

4.4 Data analysis

The species richness (*S*) of vascular plants, bryophytes and lichens for every quadrat was calculated as the number of species present in the quadrat. For vascular plant species (**II**), averaged data based on observations made in spring, summer and autumn was used in the analysis. Bryophytes and lichens were grouped based on the ecological indicator values of species according to Düll (1991) and Wirth (2010) (**III**).

An average Simpson's diversity index (*D'*) was calculated for every quadrat using PC-ORD Version 6 (McCune & Mefford 2011) (Equation 1).

$$\text{Simpson's } D' = 1 - \Sigma p_i^2 \qquad (1)$$

where p_i is the proportion of the sample belonging to the i-th species.

The Koch index (K_k) (Equation 2) was used to evaluate the homogeneity of vascular plant communities (Mirkin & Rozenberg 1983).

$$K_k = (T - N)/((M - 1)N) \qquad (2)$$

where N is the number of species in all descriptions, M is the number of all descriptions and $T = \sum_{i=1}^{M} ni$, where n_i is the number of species in description i.

Sørensen's similarity coefficient (K_s) (Equation 3) was used to compare similarities between different communities (Sørensen 1948).

$$K_s = 2a/(2a + b + c) \qquad (3)$$

where *a* is the number of common species, and *b* and *c* are the numbers of species unique to both communities (Masing 1979).

Overlapping and unique species in the different sites and zones of the dunes are illustrated in a Venn diagram created in Venny (Oliveros 2015) (**II**).

For the statistical analysis, the transects on the dunes were divided into different zones — plains before the dune (bottoms), slopes and tops — according to the relative height and angle of the quadrat. Soil characteristics were presented for five locations over the dune profile in the current thesis; in articles (**II**; **III**) the results have been presented as average values for bottom, slope and top.

Regression analyses were carried out and coefficients of determination (R^2) calculated using Statgraphics and MS Excel 2003 (**I**; **IV**). In studies **II** and **III**, Microsoft Excel 2010 was used for basic statistical analysis. Correlation analysis was performed on the condition that the data was normally distributed, while correlation coefficients (r) to determine relations between environmental variables were obtained. A level of significance of $\alpha=0.05$ was applied.

A one-way ANOVA followed by a post-hoc Tukey HSD test using the Tukey-Kramer method was applied (**II**; **III**) to determine significant differences in environmental characteristics between different zones on the dunes (Vasavada 2016).

The significance of grouping factors was tested using the Multiple Response Permutation Procedure (MRPP) (**II**; **III**) on the vascular plant species and bryophyte-lichen species data. The MRPP was introduced by Mielke *et al*. (1976) as a method of detecting differences between previously classified groups (here, zones on dunes). To correct the p-values for multiple comparisons, the Bonferroni correction was applied.

Indicator species analysis (ISA) is a method of evaluating species associated with groups of sample units (Dufrene & Legendre 1997). ISA was conducted to identify indicator species for the different zones (**II**). The statistical significance of indicator values was proven using Monte Carlo simulation. The MRPP and ISA were performed using PC-ORD Version 6 (McCune & Mefford 2011).

A linear mixed model with the free statistical software R Version 3.2.3 (R Core Team 2015) function 'lmer' in the package lme4 (Bates *et al*. 2015) (with site as a random factor) was employed to clarify the effect of environmental variables and location on species richness and total cover. A Tukey HSD test was applied where a statistically significant effect of zone was observed in order to compare group means (**II**; **III**).

Non-metric Multidimensional Scaling (NMDS) ordination was performed on the free statistical software R version 3.2.3, using the community ecology package *Vegan* (Oksanen *et al*. 2015) to analyse species distribution patterns and environmental variables correlated with species composition for vascular plant species, bryophyte and lichen species data (**II**; **III**). NMDS was run using the function 'metaMDS' (default settings) as well as Bray-Curtis dissimilarities. For fitting environmental vectors and factors onto ordination, the ‘envfit’ function was used (Oksanen 2015).

Separate analysis based on the lichen data was not performed as lichens were present in only 22% of the studied quadrats.

5. RESULTS

5.1 Environmental factors

Soil horizons

In 2007, soil horizons were distinguished on the western slopes of sites 4 and 5 to a depth of 1 m from the surface. A-horizons were present only at the bottoms of the dunes and averaged 8 cm in thickness, while O-horizons were thicker at the bottoms; average thickness here was 12.5 cm compared with 5–10 cm for the slopes and tops (**I**).

To describe soil conditions according to the cardinal directions of the slopes, in 2016 soil horizons were distinguished for up to 20 cm on sites 1, 2, 3 and 4 (Figure 2). The soil organic horizon averaged 9.1 cm on the bottom, 8 cm on the slope and 8.4 cm on the top of the dunes, with the dominant moderately decomposed organic layer forming 58.2% of the organic layer on the bottoms, 56.3% on the slopes and 67.9% on the tops (**III**).

According to the results, soils in the dunes were primarily Haplic Podzols but varied according to the zone of the dune. On site No. 1, Haplic Podzol with A-horizon was prevalent on the southern bottom; on the southern slope and top of the dune, Haplic Podzol was dominant; on the northern slope Gleyic Podzol was dominant; and on the northern bottom Gleyic Podzol with A-horizon dominated. On site No. 2 the following were dominant: Haplic Podzol on the western bottom; Haplic Podzol with A-horizon on the western slope; Haplic Podzol on the top and on the eastern slope; and Gleyic Podzol with A-horizon on the eastern bottom of the dune (**II**).

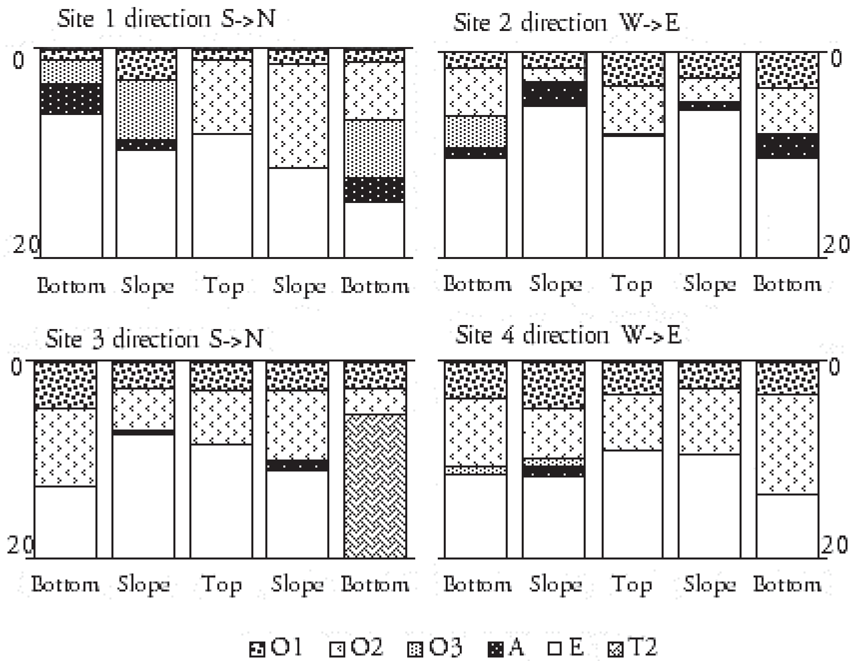

Figure 2. Soil horizons and their thicknesses (cm) up to 20 cm on different zones and sites. O1 – poorly decomposed organic horizon; O2 – moderately decomposed organic horizon; O3 – well-decomposed organic horizon; A – humus horizon; E – eluviated horizon; T2 – moderately decomposed peat horizon.

The dominant soils found on site No. 3 were: Gleyic Podzol on the southern bottom of the dune; Haplic Podzol on the southern slope and top; Haplic Podzol with A-horizon on the northern slope; and Carbi-Saprihistic Podzol on the northern bottom. For site No. 4 the results were as follows: Gleyic Podzol on the western bottom; Haplic Podzol with A-horizon on the western slope; and Haplic Podzol on the top, the eastern slope and the eastern bottom of the dune (**II**).

Soil pH and electrical conductivity

Soil pH varied among the different sites and zones of the dunes. Average soil pH was 4.3, while the minimum and maximum values estimated for the quadrats were 3.4 and 5.7 respectively (Figure 3; Table 4 in **II**; Table 2 in **III**).

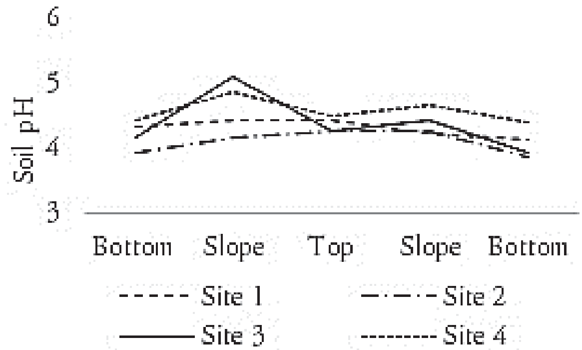

Figure 3. Soil pH at different zones and sites.

In the upper soil layer at a depth of 2 cm (O2 horizon) on the western slope of site No. 5, soil pH varied from 4.5 to 6.8. No significant dependence was revealed by regression analysis between soil pH at this depth and height of the sampling site (**IV**). Similar results were found for soil pH from the upper 20 cm soil layer and height of the quadrat (R^2_{Hrel}<0.001; R^2_{Habs}=0.01).

Soil electrical conductivity (EC) is used to obtain information about soil properties that induce plant growth. The arithmetic mean EC for the studied area was 151.3 µS cm^{-1}, the minimum value being 55.4 µS cm^{-1} and the maximum value being 724.3 µS cm^{-1} (**II**). Average electrical conductivity according to a linear mixed model for the dune bottoms studied was 185.0 µS cm^{-1}, for the tops 131.2 µS cm^{-1}, and for the slopes 140.6 µS cm^{-1} (**III**). Electrical conductivity on the bottoms of the dunes was significantly higher than that on the slopes and tops (**III**). It may be said that the bottoms of the dunes achieve higher electrical conductivity and lower soil pH values (**II**; **III**).

Soil nutrients

The contents of N, P, K, Ca and Mg in the soil varied depending on the site, transect cardinal direction and zone of the dune. On site No. 1, soil N, Ca and Mg contents were lowest at the top of the dune, the highest contents being found on the northern bottom (Figure 4). The contents of P and K were also highest on the northern bottom and lowest at the top of the dune (Figure 4; Table 4 in **II**).

On site No. 2, N content was highest on the western bottom and lowest on the eastern slope of the dune (Figure 4); P showed the highest values on the top and the lowest on the western slope of the dune (Figure 4); and K content was highest on the western bottom and lowest on the eastern slope of the dune. Soil Ca and Mg showed higher contents on the western bottom of the dune compared with other zones (Figure 4).

On site No. 3, N, P, K and Mg contents were highest on the northern bottom compared with other zones (Figure 4). Calcium content was lowest on the top of the dune, while its highest values were recorded on the northern bottom.

On site No. 4 the contents of N, P, K, Ca and Mg showed highest values on the western bottom (Figure 4). The lowest values for N content were found on the western slope; for P on the eastern bottom; for K on the eastern slope; and for Ca and Mg also on the western slope of the dune (Figure 4).

On site No.5, the western side of the dune, the highest N, K, Ca and Mg values were recorded on the bottom of the dune, the lowest values on the top (Table 1 in **I**). The content of P was highest on the top of the dune and lowest on the slope, where it was 56% lower than at the bottom of the dune (Table 1 in **I**).

Nutrient ratios are used as indicators of soil nutrient limitation (e.g. N:P ratio) and can describe changes in ground vegetation species composition (Liu *et al*. 2010). In this study the average values for N:P and N:K ratios were similar in all of the observed locations, only average Ca:Mg ratio showed statistically significant differences between bottoms and slopes.

The average N:P ratio was 136.2 on the tops (ranging from 33.8 to 548.2), 141.9 on the slopes (ranging from 26.4 to 466.1) and 147.2 at the bottoms (ranging from 70.6 to 425.1) of the dunes (Table 2 in **III**).

The average N:K ratio for the tops was 40 (minimum value 21.1 and maximum value 60.4), for the slopes 39 (minimum 22.1 and maximum 132.3) and for the bottoms 41.2 (minimum 21.2 and maximum 83.8) (Table 2 in **III**).

The average Ca:Mg ratio at the tops of the dunes was 5.1 (the minimum and the maximum absolute values being respectively 3.1 and 6.6); on the slopes 6 (minimum and maximum respectively 2.8 and 20.7) and on the bottoms 3.9 (minimum and maximum respectively 1.2 and 7.9) (Table 2 in **III**).

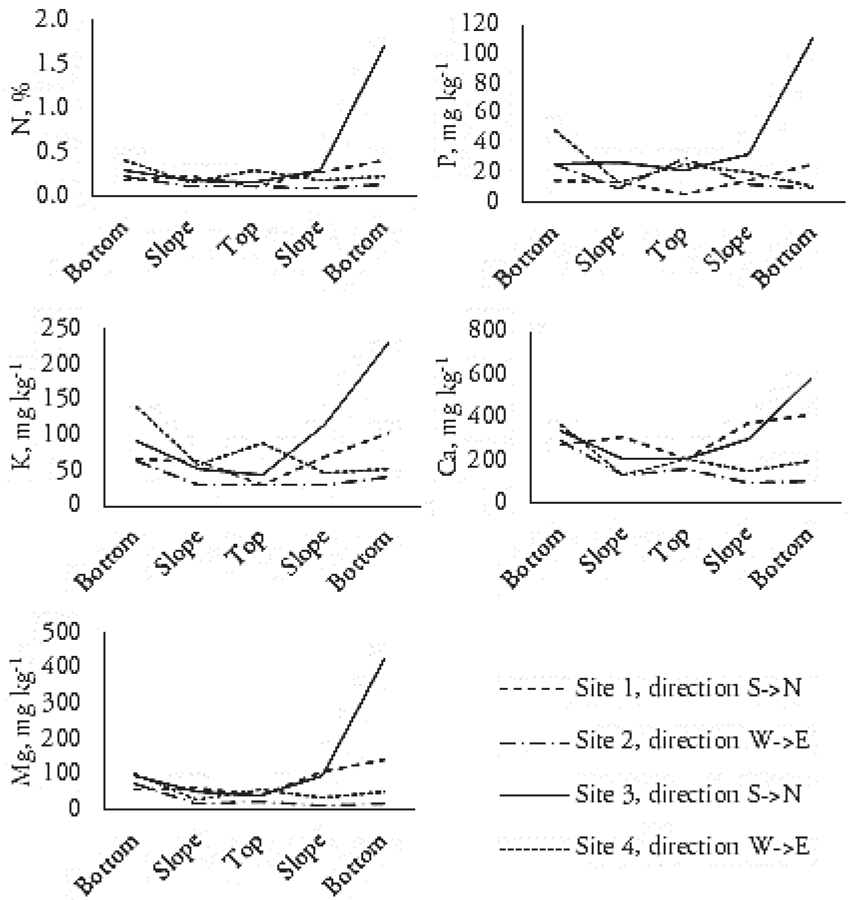

Figure 4. Contents of N, P, K, Ca and Mg in different sites and zones on dunes.

Average soil moisture values showed positive correlations with the contents of N ($r=0.841$), P ($r=0.706$), K ($r=0.705$), Ca ($r=0.568$) and Mg ($r=0.811$) in the dune soil.

Soil moisture conditions

Average soil volumetric water content based on measurements throughout the growing season on dunes was 8.2%. The highest absolute value was 48.6%, measured in spring at the bottom of site 3, while the lowest value was 0.7% recorded on the upper part of the slope of site 2 also in spring (**II**).

Soil volumetric water content was seasonally changeable, showing statistically significant ($p<0.01$) differences between spring, summer and autumn (**II**). The highest average soil moisture occurred in autumn, at 12.7%, while the driest period was spring when average soil moisture was only 4.6%. The average soil moisture in summer was 7.3% (Figure 5; Table 4 in **II**).

Average and seasonal average soil water contents showed significant differences with respect to zones on the dunes (Table 4 in **II;** Table 2 in **III**). For average soil volumetric content, the driest quadrats were located on the tops of the dunes (**I**; **II**), the bottoms of the dunes being 48% moister than the tops (**III**).

Average soil VWC on the north-facing quadrats was significantly higher compared with that on the south-, east- and west-facing quadrats ($p < 0.01$). Differences between soil volumetric water contents on the southern, western and eastern quadrats were not statistically significant ($p > 0.05$) (**III**).

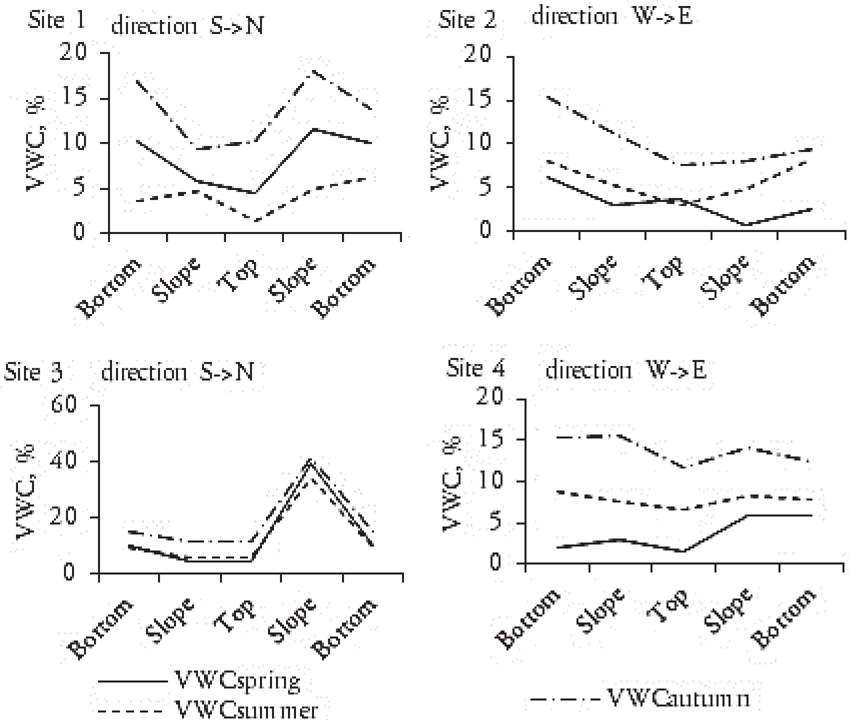

Figure 5. Soil volumetric water content (VWC, %) in spring, summer and autumn in different sites and zones on dunes.

Average soil volumetric water content in summer and autumn showed a negative correlation with relative height of the dunes (r_{sum}=-0.53 and r_{aut}=-0.54). Soil volumetric water content in autumn was also negatively correlated with absolute height of the dunes (r_{aut}=-0.52). However, soil volumetric water content was not correlated with differently decomposed soil litter horizon thicknesses (r<0.1).

Light conditions

Light conditions varied along the transect over the dunes (Figure 6), with average PAR on the dunes at 450.2 μmol $m^{-2}s^{-1}$ and average canopy cover 0.5.

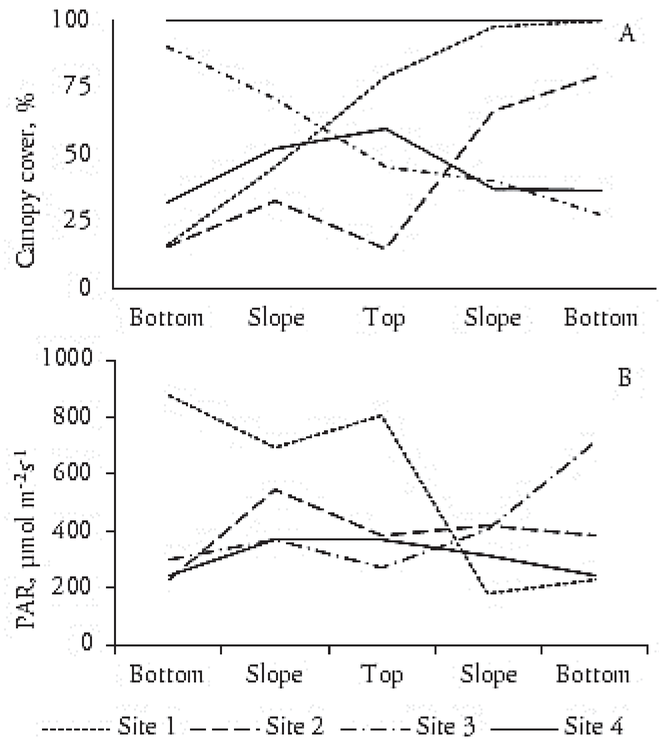

Figure 6. Average canopy cover (A) and PAR (B) values in different sites and zones on dunes.

Average canopy cover was negatively correlated (r_{CC}=-0.67) with aspect of the quadrat, being higher on the northern and eastern quadrats and lower on the southern and western ones (**III**). Average canopy cover on the slopes was significantly higher than canopy cover at the bottoms and tops of the dunes (Table 2 in **III**). Average PAR was highest on the southern slopes, with an average value of 667.4 2 μ mol $m^{-2}s^{-1}$, and significantly higher than the average PAR on northern, eastern and western slopes ($p<0.001$).

5.2 Ground vegetation

In total, 133 ground vegetation species were determined in the study area (**I**; **II**; **III**; **IV**). *Vaccinium vitis-idaea* was the most frequent species found, being present in 82% of the quadrats. This was followed by *Vaccinium myrtillus* at 72%, *Deschampsia* *flexuosa* at 71% and *Melampyrum pratense* L. at 70% of the quadrats. During earlier research (in 2004 and 2006) on the western slope of site No. 5, 20 vascular plant species (including seedlings of *Sorbus aucuparia* L., *Frangula alnus* Mill. and *Picea abies* (L.) H. Karst.), 26 species of lichens and 38 species of bryophytes were recorded (**I**; **IV**).

The most frequent species on site No. 5 were *Deschampsia flexuosa*, *Vaccinium vitis-idaea*, *Melampyrum pratense* (Table 3), *Hylocomium splendens*, *Pleurozium schreberi*, *Dicranum scoparum* (Hedw.) and spp. *Cladonia* Hill ex P. Browne. Because of differences in the methodology used, bryophytes and lichens on site No. 5 are excluded from Table 3, and instead the list of species can be found in **IV**, Appendix 1.

On site No. 5, the species number at the bottom of the dune was four times higher than that on the top. At the bottom, *Vaccinium myrtillus*, *Oxalis acetosella* L. and *Deschampsia flexuosa* were the most abundant; on the top, xerophytic species such as *Festuca ovina* L. and *Crepis tectorum* L. were present (**I**). The total cover of vascular plant species, bryophytes and lichens varied on the dune slope (**I**). According to the study conducted in 2004, a clear zonation of ground vegetation was recorded on the western slope and 12 bryophyte and lichen zones determined (**IV**). However, as previously mentioned, the bryophyte and lichen species information was left out of further statistical analyses because of methodological differences.

In 2008, on the first four dunes (sites No. 1—4) and covering 232 quadrats, 87 different vascular plant species, bryophytes and lichens were distinguished (Table 3). Thirty-four species of vascular plants belonging to 18 genera were found (**II**). The most commonly represented family was *Poaceae* with four species, followed by *Asteraceae*, *Ericaceae*, *Juncaceae*, *Liliaceae* and *Vaccinaceae*, all with three species.

The most frequent species on site No. 1 was *Deschampsia flexuosa* (58 quadrats), on site No. 2 *Deschampsia flexuosa* (92 quadrats), on site No. 3 *Melampyrum pratense* (27 quadrats) and on site No. 4 *Vaccinium vitis-idaea* (34 quadrats). Four quadrats had no vascular plant species (1.7% of all quadrats). Thirteen different species of vascular plants were distinguished as dominants in the quadrats (**II**). *Vaccinium myrtillus* was the dominant vascular plant species in 68 of the 232 quadrats (29.3%), followed by *Deschampsia flexuosa* (27.2%) and *Vaccinium vitis-idaea* (16.4%).

Fifty-two species of bryophytes and lichens were determined in the quadrats (30 bryophyte species from 12 genera and 22 lichen species from two genera) (Table 3) (**III**). Bryophytes were recorded on all 232 quadrats, but lichens were present in only 50 (**III**). Four species were found on the additional quadrats: lichen *Cladonia cornuta* (L.) Hoffm. and bryophytes *Cephaloziella hampeana* (Nees) Schiffn., *Ptilidium pulcherrimum* (Weber) Vain. and *Scleropodium purum* (Hedw.) Limpr. *P.* The most represented bryophyte families were *Brachytheciaceae* (eight species) and *Dicranaceae* (six species). The family *Cladoniaceae* was the dominant one among the lichens (21 species).

The most frequent bryophytes found were *Pleurozium schreberi*, *Dicranum polysetum* Sw. ex anon. and *Hylocomium splendens*. The most common lichens were *Cladonia arbuscula* (Wallr.) Flot., *Cladonia furcata* (Huds.) Schrad., *Cladonia rangiferina* (L.) F.H. Wigg. and *Cladonia stygia* (Fr.) Ruoss (**III**). *Pleurozium schreberi* was the dominant species in the bryophyte-lichen layer on all sites, being the dominant bryophyte species in 128 of the 232 quadrats. Lichens were dominant in seven quadrats on sites No. 1 and 2, the dominant species being *Cladonia squamosa* Hoffm., *Cladonia arbuscula*, *Cladonia rangiferina* and *Cladonia stygia (***III***)*.

The dominant associations in the vascular plant and bryophyte-lichen layers were as follows: *Vaccinium myrtillus – Pleurozium schreberi* (34 quadrats), *Deschampsia flexuosa – Pleurozium schreberi* (33 quadrats), *Vaccinium myrtillus – Hylocomium splendens* (29 quadrats), *Vaccinium vitis-idaea – Pleurozium schreberi* (27 quadrats) and *Deschampsia flexuosa – Hylocomium splendens* (20 quadrats). Altogether there were 39 different dominant vascular plant and bryophyte-lichen layer associations, 18 of them occurring in only one quadrat.

Table 3. List of species and their occurrence on quadrats at different sites (**I**, **II**, **III**). The list of bryophyte and lichen species on site No. 5 is presented in **IV**, Appendix 1.

Vascular plant species	Site 1	Site 2	Site 3	Site 4	Site 5	All Sites	%
Aegopodium podagraria	1					1	0.4
Arctostaphylos uva-ursi	1	1				2	0.8
Calamagrostis arundinacea					4	4	1.6
Calamagrostis epigeios					1	1	0.4
Calluna vulgaris	14	49	1	12	6	82	32.7
Campanula patula		2				2	0.8
Carex caryophyllea		1				1	0.4
Carex digitata	2					2	0.8
Convallaria majalis	5	3			4	12	4.8
Crepis tectorum					2	2	0.8
Deschampsia caespitosa	2					2	0.8
Deschampsia flexuosa	58	92	12		17	179	71.3
Dryopteris carthusiana					1	1	0.4
Empetrum nigrum	12	9	1	7		29	11.6
Epilobium angustifolium	3	2				5	2.0
Festuca ovina					3	3	1.2
Festuca polesica	20	40	18	10		88	35.1
Festuca rubra		22	11			33	13.1
Hieracium umbellatum		5				5	2.0
Ledum palustre			7			7	2.8
Luzula campestris		6				6	2.4
Luzula multiflora		3				3	1.2
Luzula pilosa	20	7	11			38	15.1
Lycopodium annotinum	2	1				3	1.2
Lycopodium clavatum		1				1	0.4
Lysimachia vulgaris					1	1	0.4
Maianthemum bifolium	17					17	6.8
Melampyrum pratense	49	60	27	29	10	175	69.7
Monotropa hypopitys		1				1	0.4
Mycelis muralis	3					3	1.2
Oxalis acetosella	8				4	12	4.8
Polygonatum odoratum	1	9				10	4.0
Rubus idaeus	5					5	2.0

Rubus saxatilis					2	2	0.8
Sedum acre					1	1	0.4
Silene dioica		1				1	0.4
Solidago virgaurea		6			2	8	3.2
Stellaria graminea	1					1	0.4
Trientalis europaea	22	10	11		3	46	18.3
Vaccinium myrtillus	52	80	16	24	9	181	72.1
Vaccinium uliginosum	1			5		6	2.4
Vaccinium vitis-idaea	50	83	25	34	13	205	81.7
Lichens	Site 1	Site 2	Site 3	Site 4		All Sites	%
Cetraria islandica		1				1	0.4
Cladonia arbuscula		11	2	2		15	6.5
Cladonia ciliata		5		3		8	3.5
Cladonia mitis		4				4	1.7
Cladonia portentosa		1				1	0.4
Cladonia rangiferina	1	10				11	4.7
Cladonia stellaris			1	3		4	1.7
Cladonia stygia		8		3		11	4.7
Cladonia acuminata		2				2	0.9
Cladonia cariosa		1				1	0.4
Cladonia chlorophaea	3	2				5	2.2
Cladonia coniocraea	1					1	0.4
Cladonia cryptochlorophaea		1				1	0.4
Cladonia fimbriata	7					7	3.0
Cladonia furcata	3	9				12	5.2
Cladonia ochrochlora		1				1	0.4
Cladonia pyxidata	1					1	0.4
Cladonia rangiformis		2				2	0.9
Cladonia rei		1				1	0.4
Cladonia scabriuscula	2					2	0.9
Cladonia squamosa	1	1				2	0.9
Cladonia subulata		1				1	0.4
Bryophytes	Site 1	Site 2	Site 3	Site 4		All Sites	%
Aulacomnium palustre		2				2	0.9
Aulacomnium palustre var. imbricatum		1				1	0.4

Brachythecium albicans	1					1	0.4
Brachythecium erythrorrhizon	2		1			3	1.3
Brachythecium oedipodium	4		1	1		6	2.6
Brachythecium starkei	2	3	3			8	3.4
Campylium sommerfeltii		3				3	1.3
Campylium stellatum		1				1	0.4
Cephalozia bicuspidata		1				1	0.4
Cephaloziella rubella	1	2				3	1.3
Ceratodon purpureus	9	3				12	5.2
Cirriphyllum piliferum			1			1	0.4
Dicranum bonjeanii	7	5	6	1		19	8.2
Dicranum flagellare		1				1	0.4
Dicranum majus		1				1	0.4
Dicranum polysetum	28	50	12	29		119	51.0
Dicranum scoparium	10	8	4	25		47	20.0
Drepanocladus aduncus			1			1	0.4
Eurhynchium angustirete	1					1	0.4
Eurhynchium praelongum		1				1	0.4
Eurhynchium pulchellum	2	2	1			5	2.2
Hylocomium splendens	37	87	15	9		148	64
Lophozia excisa		1				1	0.4
Plagiomnium affine	1					1	0.4
Plagiomnium medium	1					1	0.4
Plagiothecium laetum		1				1	0.4
Pleurozium schreberi	50	94	32	33		209	90.0
Pohlia nutans	2					2	0.9
Ptilidium ciliare				3		3	1.3
Ptilium crista-castrensis	3	5	1	5		14	6.0
Rhytidiadelphus triquetrus	2	1				3	1.3

Simpson's diversity index (*D'*) was evaluated according to vascular plant, bryophyte and lichen species data for every quadrat and averaged values calculated based on their zones on dunes (Figure 7; Table 3 in **III**).

The highest vascular plant species richness was recorded on the bottoms of the dunes, while the lowest vascular plant species richness was found on the slopes of dunes No. 1—4 (Table 4).

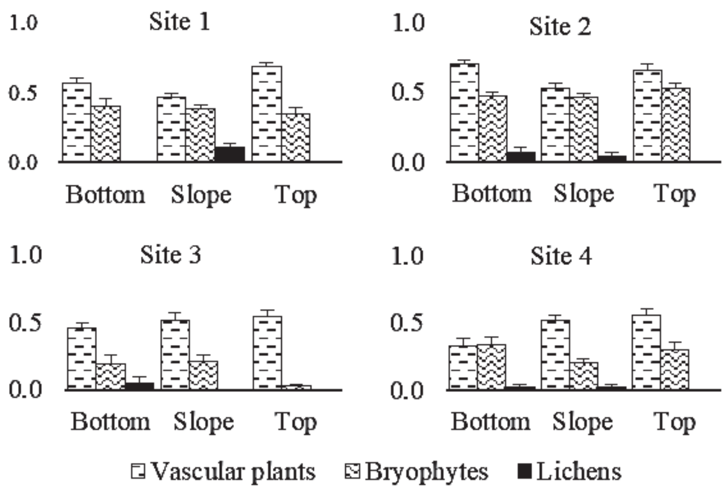

Figure 7. Average bryophyte, vascular plant and lichen species Simpson's diversity indexes for different zones on dunes.

Bryophyte species richness was also higher on the bottoms of the dunes and decreased toward the tops, showing no statistically significant difference between species richness on the slopes and on the tops of the dunes (Table 4; Table 3 in **III**).

Table 4. Average species richness at different zones on dunes, with minimum and maximum values for vascular plants (S_{vasc}), bryophytes (S_{bryo}) and lichens (S_{lich}) according to a linear mixed model (Table 3 in **III**). Letters denote significant differences between zones in accordance with the post-hoc Tukey HSD test.

Zone	S_{vasc}			S_{bryo}			S_{lich}		
	Mean ± St.err	Min	Max	Mean ± St.err	Min	Max	Mean ± St.err	Min	Max
Bottom	5.2±0.6^{b}	2	11	3.0±0.2^{b}	1	6	0.1±0.1^{a}	0	3
Slope	4.3±0.5^{a}	0	11	2.6±0.1^{a}	1	5	0.5±0.1^{b}	0	6
Top	4.9±0.6^{ab}	2	9	2.5±0.2^{a}	1	4	0.1±0.2^{a}	0	1

As far as lichen species richness was concerned, the number of species was highest on the slopes of the dunes, while the bottoms and tops of the dunes showed similar and significantly lower lichen species richness (Table 4; Table 3 in **III**).

The community similarity coefficient (Sørensen's similarity coefficient) indicated that the lower and higher dunes were similar in terms of vascular plant species occurrence (K_s=0.4 for higher dunes and K_s=0.4 for lower dunes).

According to the Koch index, the highest homogeneity of vascular plant species communities occurred on the lower dunes, i.e. sites No. 3 and No. 4 (respectively 38% and 49%). On the higher dunes, i.e. sites No. 1 and No. 2, the Koch index was 17% and 24%, respectively.

A multiple response permutation procedure based on vascular plant data on different dunes indicated that the lower dunes did not differ in vascular plants species composition (**II**). The same conclusions could be drawn for the bryophyte and lichen data: species composition was similar on dunes 3 and 4, both of which were defined as lower dunes (Table 5). But when all species (vascular plants, bryophytes and lichens) were analysed together, all sites differed significantly from each other according to the MRPP test (Table 5).

Table 5. The results of multiple response permutation procedure (MRPP) tests comparing ground vegetation ($p\text{-value}_{allsp}$), vascular plant species ($p\text{-value}_{vascsp}$), bryophyte and lichen ($p\text{-value}_{bryolich}$) and bryophyte ($p\text{-value}_{bryo}$) species composition on different dunes (Table 2 in **II**).

Test pair	Sites 1 vs. 2	Sites 1 vs. 3	Sites 1 vs. 4	Sites 2 vs. 3	Sites 2 vs. 4	Sites 3 vs. 4
$p\text{-value}_{allsp}$	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.005**
$p\text{-value}_{vascsp}$	**<0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**	0.011
$p\text{-value}_{bryolich}$	**0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.02
$p\text{-value}_{bryo}$	**0.002**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.02

*Bold values are significant after Bonferroni correction

According to the MRPP test based on zones on the dunes (Table 6), ground vegetation communities differed between the bottoms, slopes and tops, showing statistically important differences in species composition ($p<0.05$). Similar results were obtained when only vascular plants species were analysed; here too the MRPP indicated that species composition differed significantly between zones (Table 6).

According to MRPP based on zone, bryophyte and lichen communities were significantly different on the bottoms versus the tops and on the slopes versus the tops of dunes, while the bottoms and slopes were similar (Table 6). When bryophytes were analysed separately, it was the slopes and tops that were similar while the bottoms versus the slopes and the bottoms versus the tops showed significant differences (**III**).

Table 6. The results of MRPP tests comparing ground vegetation ($p\text{-value}_{allsp}$), vascular plant ($p\text{-value}_{vascsp}$), bryophyte-lichen ($p\text{-value}_{bryolich}$) and bryophyte ($p\text{-value}_{bryo}$) species composition in different zones of the dunes.

Test pair	Bottom vs. Slope	Bottom vs. Top	Slope vs. Top
$p\text{-value}_{allsp}$	**0.01**	**0.0002**	**0.003**
$p\text{-value}_{vascsp}$	**<0.001**	**<0.001**	**0.006**
$p\text{-value}_{bryolich}$	0.535	**0.015**	**0.012**
$p\text{-value}_{bryo}$	**0.001**	**0.002**	0.263

*Bold values are significant after Bonferroni correction

ISA based on all ground vegetation data revealed indicator species for the bottoms, slopes and tops of the dunes (Table 7). On the slopes of the dunes, the indicator species were lower in number and belonged to the bryophyte-lichen layer: *Ceratodon purpureus* (Hedw.) Broth., *C. arbuscula*, *C. rangiferina* and *C. stygia*.

When only the vascular plant species data for the different sites was analysed, the indicator species for the bottoms and slopes were different for each dune. That said, *C. vulgaris* was identified as an indicator species for the tops of three dunes, *Festuca rubra* for two (Table 3 in **II**).

When all the dunes were analysed together, nine vascular plant species were identified as indicator species for the bottoms (*C. majalis, L. palustre, M. bifolium, M. muralis, O. acetosella, R. idaeus, V. myrtillus, V. uliginosum* and *V. vitis-idaea*). For the tops, the indicator species identified were *C. vulgaris, F. rubra, H. umbellatum, M. pratense* and *S. virgaurea.* No vascular plant species were recognised as being indicator species for the slopes of the dunes.

With regard to the bryophyte and lichen layer, indicator species analysis identified characteristic species for zones on dunes, such as *Brachythecium erythrorrhizon*, *Brachythecium oedipodium* and *Hylocomium splendens* for the bottoms, *Ceratodon purpureus*, *Cladonia rangiferina* and *Cladonia stygia* for the slopes and *Pleurozium schreberi* for the tops (**III**).

Table 7. Indicator species for different zones on the dunes with statistically important indicator values ($p<0.05$).

Species	Zone on dune	p-value	Indicator value
Vaccinium myrtillus	Bottom	0.0002	45.8
Vaccinium vitis-idaea	Bottom	0.0010	45.5
Rubus idaeus	Bottom	0.0020	9.6
Convallaria majalis	Bottom	0.0092	9.5
Vaccinium uliginosum	Bottom	0.0102	7.5
Ledum palustre	Bottom	0.0108	8.2
Brachythecium erythrorrhizon	Bottom	0.0134	5.8
Oxalis acetosella	Bottom	0.0162	8.9
Maianthemum bifolium	Bottom	0.0164	11.7
Mycelis muralis	Bottom	0.0188	5.8
Hylocomium splendens	Bottom	0.0246	32.0
Brachythecium oedipodium	Bottom	0.0400	6.7
Ceratodon purpureus	Slope	0.0322	8.5
Cladonia rangiferina	Slope	0.0470	7.7
Cladonia stygia	Slope	0.0498	7.7
Cladonia arbuscula	Slope	0.0504	9.5
Festuca rubra	Top	0.0002	25.8
Calluna vulgaris	Top	0.0004	35.9
Hieracium umbellatum	Top	0.0010	10.3
Solidago virgaurea	Top	0.0024	9.9
Pleurozium schreberi	Top	0.0062	38.7
Melampyrum pratense	Top	0.0078	39.2

5.3 Environmental factors affecting species richness, species composition and cover

5.3.1 Vascular plant species

The results of the preliminary study in 2006 indicated, according to regression analysis, that the number of vascular plant species on the western slope of site No. 5 was related to the location of the sample plot, soil pH and soil volumetric water content, and N, K, Ca and Mg content (**I**). On site No. 4, which had a lower relative and absolute height, no relationships between the number of species and the environmental factors studied were revealed (**I**).

Based on the results of the more detailed study in 2008 (**II**), a linear mixed model determined that the zone on the dune, the aspect of the quadrat, light conditions (PAR), soil pH, soil volumetric water content and total N and K content were the main factors affecting vascular plant species richness in the quadrats at sites 1, 2, 3 and 4 (Table 5 in **II**).

With regard to total cover of vascular plant species the same factors were important, with the exception of PAR and aspect of the quadrat. In addition, the absolute height of the quadrat and the thickness of the litter horizon had a significant impact on the total cover of vascular plant species (Table 5 in **II**).

The results of the NMDS analysis (stress 0.208) indicated that vascular plant species composition was affected by site-specific factors such as the transect direction, the absolute height of the quadrat, canopy cover, cover of lichens and bryophytes, soil volumetric water content and N, K and Mg content (Figure 4 in **II**).

5.3.2 Bryophytes and lichens

The most important factors influencing bryophyte and lichen species composition at sites 1, 2, 3 and 4 were height and aspect of quadrat, PAR, vascular plant total cover and various soil characteristics including volumetric water content, pH, electrical conductivity and thickness of the moderately decomposed litter layer (Table 5 and Figure 4 in **III**). On site 5, according to correlation analysis the number of lichen species was strongly related to the height of the zone, the number of lichens increasing with height growth (**IV**). On the western slope of site 5, bryophyte species richness was not correlated with height of the dune, nor was the number of bryophyte and lichen species related to soil pH (**IV**).

According to the ecological indicator values (Düll 1991), the majority of bryophyte species were light-demanding species (Fig. 2 A in **III**). The moisture preference of bryophyte species was variable, the most frequent values on the moisture index varying between 4 and 7, referring to the preference for moderately dry to moist habitats and based on pH indices assigned to bryophyte species, the majority of species preferred acidic substrate (Fig. 2 A in **III**).

Light indicator values (according to Wirth 2010) were not available for 36% of the lichen species. However, according to available indices the lichens were mainly light-demanding species (the most frequent values on the light index being 7 and 8) (Fig. 2 B in **III**). Based on moisture and substrate pH indices, the highest number of lichen species were those with broad amplitude; however, both moisture and substrate pH indices were unavailable for eight species (Fig. 2 B in **III**).

The species composition of bryophytes was, according to the NMDS analysis, most significantly influenced by site, aspect of the quadrat, PAR, vascular plant total cover, soil pH, soil volumetric water content, soil electrical conductivity and thickness of the moderately decomposed litter horizon (Table 5 in **III**; Figure 8). A separate analysis of lichen species composition and richness was not performed as lichens were present in only 22% of the quadrats studied (**III**).

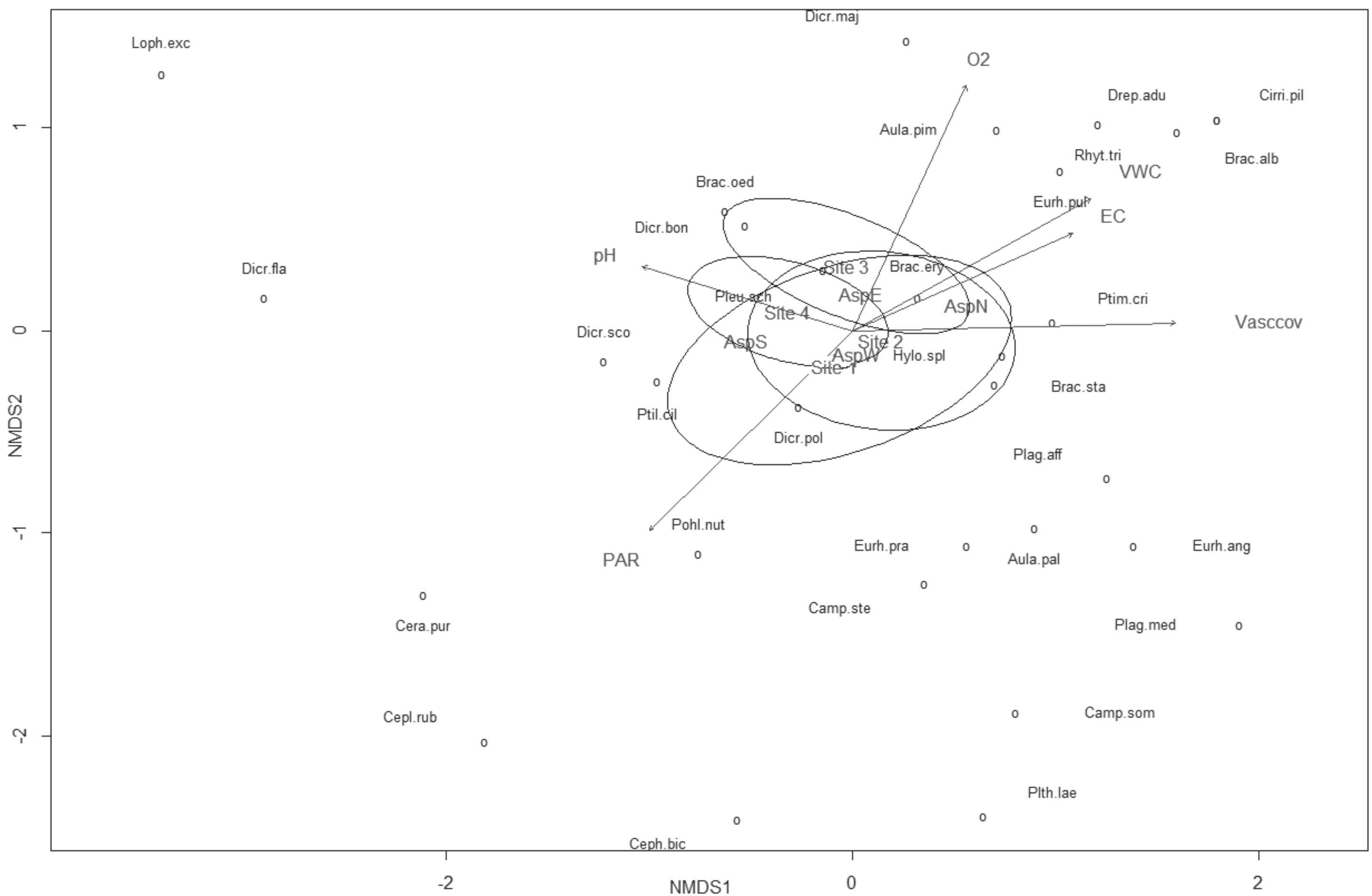

Figure 8. NMDS ordination (stress 0.140), based on the abundance of bryophytes; arrows indicate the environmental factors

that were the most significantly (p=0.001) related to the ordination. Environmental factors: Asp - aspect of the quadrat; EC - average electrical conductivity (μS cm^{-1}); pH - average soil pH; VWC - average soil water content (%); PAR - photosynthetically active radiation (μ mol $m^{-2}s^{-1}$); O2 - average thickness of the moderately decomposed organic horizon (cm); Vasccov - cover of vascular plants (%). List of bryophyte species: Aula. pal – *Aulacomnium palustre*; Aula. pim – *Aulacomnium palustre var. imbricatum*; Brac. alb – *Brachythecium albicans*; Brac. ery – *Brachythecium erythrorrhizon*; Brac. oed – *Brachythecium oedipodium*; Brac. sta – *Brachythecium starkei*; Camp. som – *Campylium sommerfeltii*; Camp. ste – *Campylium stellatum*; Ceph. bis – *Cephalozia bicuspidata*; Ceph. rub – *Cephaloziella rubella*; Cera. pur – *Ceratodon purpureus*; Cirr. pil – *Cirriphyllum piliferum;* Dicr. bon – *Dicranum bonjeanii*; Dicr. fla – *Dicranum flagellare*; Dicr. maj – *Dicranum majus*; Dicr. pol – *Dicranum polysetum*; Dicr. sco – *Dicranum scoparium*; Drep. adu – *Drepanocladus aduncus*; Eurh. ang – *Eurhynchium angustirete*; Eurh. pra – *Eurhynchium praelongum*; Eurh. pul – *Eurhynchium pulchellum*; Hylo. spl – *Hylocomium splendens*; Loph. exc – *Lophozia excisa*; Plag. aff – *Plagiomnium affine*; Plag. med – *Plagiomnium medium*; Plag. lae – *Plagiothecium laetum*; Pleu. sch – *Pleurozium schreberi*; Pohl. nut – *Pohlia nutans*; Ptil. cil – *Ptilidium ciliare*; Ptil. crc – *Ptilium crista-castrensis*; Rhyt. tri – *Rhytidiadelphus triquetrus*.

5.3.3 Ground vegetation (vascular plant species, bryophytes and lichens)

Ground vegetation species composition on the dunes at sites 1, 2, 3 and 4 was found to be affected by various environmental variables (Table 8 and Figure 10). Significantly important factors that were revealed by NMDS analysis were: site-related — relative height and aspect of the quadrat; soil-related — thickness of the moderately decomposed litter horizon, soil pH, soil volumetric water content, content of K and Ca; and light-related — canopy cover and PAR.

Table 8. Relationships between ground vegetation species composition and environmental vectors and factors on dunes, according to non-metric multidimensional scaling ordination.

Vectors	R^2	Pr (>r)
Relative height (m)	0.06	0.001***
Below-canopy photosynthetically active radiation (μ mol $m^{-2}s^{-1}$)	0.17	0.001***
Average soil volumetric water content (%)	0.13	0.001***
Average electrical conductivity (µS cm^{-1})	0.11	0.001***
Canopy cover (%)	0.14	0.001***
Organic horizon thickness (cm) of moderately decomposed soil	0.15	0.001***
Potassium content (mg kg^{-1})	0.06	0.001***
Calcium content (mg kg^{-1})	0.08	0.001***
Absolute height (m.a.s.l)	0.05	0.002**
Average pH_{H2O}	0.07	0.003**
Magnesium content (mg kg^{-1})	0.06	0.004**
Total nitrogen content (%)	0.04	0.016*
Organic horizon thickness (cm) of poorly decomposed soil	0.03	0.023*
Organic horizon thickness (cm) of well-decomposed soil	0.02	0.067
Phosphorus content (mg kg^{-1})	0.02	0.099
Degree of inclination or ascent (°)	0.01	0.335
Humus horizon thickness (cm)	0.01	0.388
Factors		
Site	0.09	0.001***
Aspect of the quadrat	0.20	0.001***
Zone on dune	0.04	0.003**

Significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Three dominant species associations of ground vegetation that occurred more than once at higher litter horizon thicknesses (where the litter horizon exceeded the average value of 7.4 cm on all sites) were: *Empetrum nigrum* – *Pleurozium schreberi*, *Vaccinium uliginosum* – *P. schreberi* and *E. nigrum* – *Hylocomium splendens* (Table 9).

Table 9. Dominant species associations that occurred more than once in the study sites where the litter horizon thickness exceeded the average value of 7.4 cm.

Dominant species associations	No. of quadrats	O1	O2	O3	O
Empetrum nigrum–Pleurozium schreberi	4	2.5	7.8	1.0	11.3
Vaccinium uliginosum–Pleurozium schreberi	2	3.0	8.0	0.0	11.0
Empetrum nigrum–Hylocomium splendens	7	1.7	7.9	1.1	10.7
Calluna vulgaris–Hylocomium splendens	3	2.7	5.0	1.3	9.0
Vaccinium vitis-idaea–Pleurozium schreberi	27	2.7	4.2	1.6	8.5
Deschampsia flexuosa–Dicranum scoparium	2	3.8	0.0	4.5	8.3
Melampyrum pratense–Pleurozium schreberi	11	2.9	4.7	0.2	7.8
Festuca polesica–Pleurozium schreberi	5	3.0	4.8	0.0	7.8
Vaccinium myrtillus–Dicranum polysetum	2	1.0	6.5	0.0	7.5
Vaccinium myrtillus–Hylocomium splendens	29	2.8	4.6	0.1	7.4

O1 – organic horizon (cm) of poorly decomposed soil; O2 – organic horizon (cm) of moderately decomposed soil; O3 – organic horizon (cm) of well-decomposed soil; O – average thickness (cm) of soil organic horizon.

Litter horizon thickness was variable in quadrats with different dominant species in the vascular plant and bryophyte-lichen layers (Figure 9 A and B).

For the vascular plant layer, the thickest O-horizon appeared in quadrats where *Convallaria majalis* and *Maianthemum bifolium* were dominant. The thinnest litter layer was recorded in quadrats where no vascular plant species were present and quadrates, where *Luzula multiflora* was dominant.

In the bryophyte-lichen layer, the thickest O-horizon was present under *Ptilium crista-castrensis* and *Eurhynchium pulchellum*. The thinnest litter layer appeared in quadrats in which *Cladonia* species were dominant.

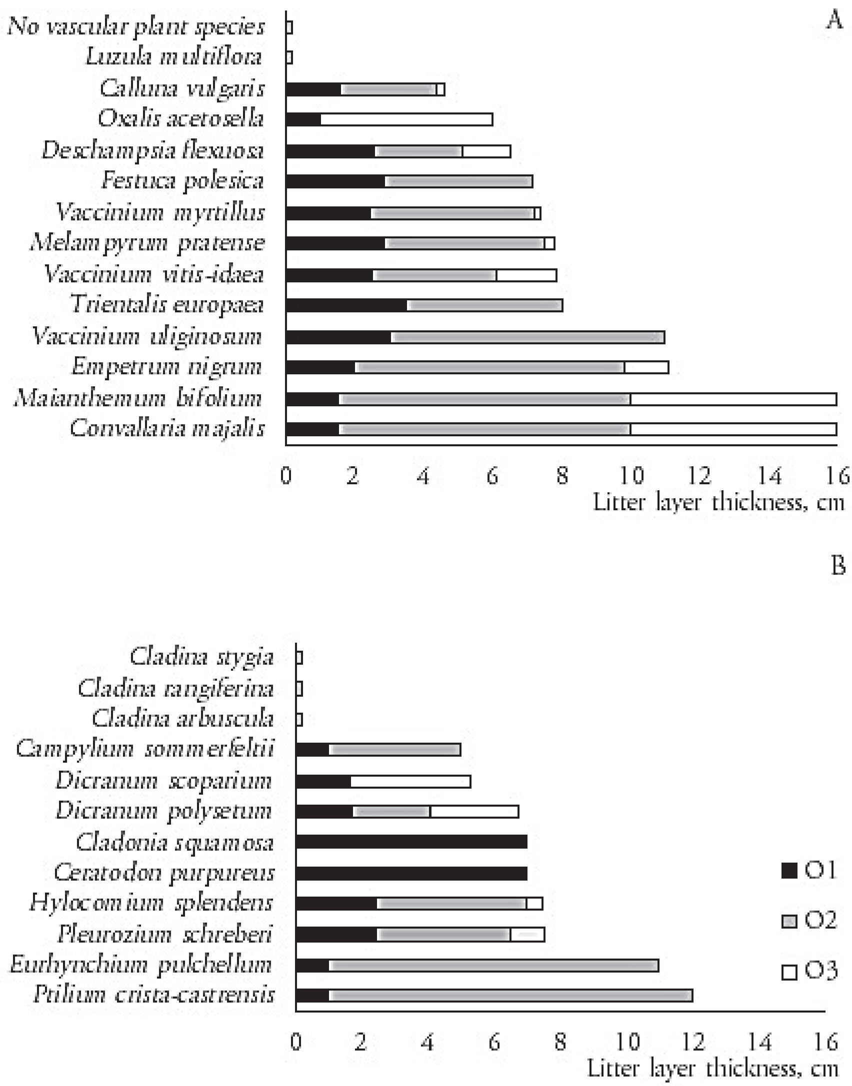

Figure 9. Differently decomposed litter layer thicknesses (cm) under different dominant species in the vascular plant (A) and bryophyte-lichen (B) layers. O1 – organic horizon (cm) of poorly decomposed soil; O2 – organic horizon (cm) of moderately decomposed soil; O3 – organic horizon (cm) of well-decomposed soil.

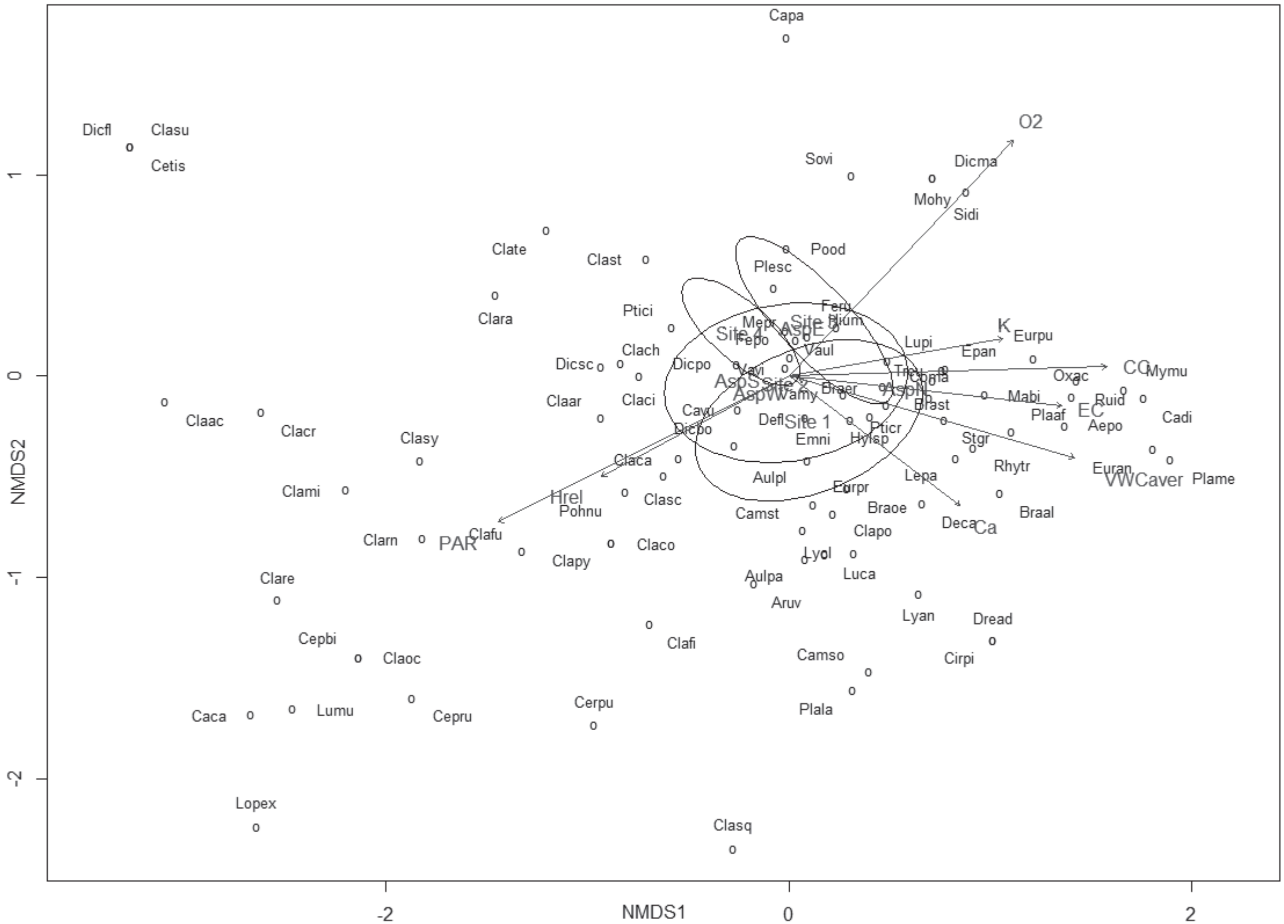

Figure 10. NMDS ordination (stress=0.219), based on the abundance data of vascular plants, bryophytes and lichens;

the arrows indicate the environmental vectors that were the most significantly ($p=0.001$) related to the ordination. Environmental factors: Asp – aspect of the quadrat. Environmental vectors: EC – average conductivity ($\mu S\ cm^{-1}$); CC – canopy cover (%); VWC_{aver} – average soil water content (%); K – potassium content ($mg\ kg^{-1}$); Ca – calcium content ($mg\ kg^{-1}$); PAR – photosynthetically active radiation ($\mu mol\ m^{-2}s^{-1}$); O2 – average thickness of the O2 horizon (cm) and H_{rel} – relative height of the quadrat (m). List of vascular plant, lichen and bryophyte species: Aepo – Aegopodium podagraria; Aruv – Arctostaphylos uva-ursi; Cavu – *Calluna vulgaris*; Capa – *Campanula patula*; Caca – *Carex caryophyllea*; Cadi – *Carex digitata*; Coma – *Convallaria majalis*; Deca – *Deschampsia caespitosa*; Defl – *Deschampsia flexuosa*; Emni – *Empetrum nigrum*; Epan – *Epilobium angustifolium*; Fepo – *Festuca polesica*; Feru – *Festuca rubra*; Hium – *Hieracium umbellatum*; Lepa – *Ledum palustre*; Luca – *Luzula campestris*; Lumu – *Luzula multiflora*; Lupi – *Luzula pilosa*; Lyan – *Lycopodium annotinum*; Lycl – *Lycopodium clavatum*; Mabi – *Maianthemum bifolium*; Mepr – *Melampyrum pratense*; Mohy – *Monotropa hypopitys*; Mymu – *Mycelis muralis*; Oxac – *Oxalis acetosella*; Pood – *Polygonatum odoratum*; Ruid – *Rubus idaeus*; Sidi – *Silene dioica*; Sovi – *Solidago virgaurea*; Stgr – *Stellaria graminea*; Treu – *Trientalis europaea*; Vamy – *Vaccinium myrtillus*; Vaul – *Vaccinium uliginosum*; Vavi – *Vaccinium vitis-idaea*; Aulpa – *Aulacomnium palustre*; AulpI – *Aulacomnium palustre var. imbricatum*; Braal – *Brachythecium albicans*; Braer – *Brachythecium erythrorrhizon*; Braoe – *Brachythecium oedipodium*; Brast – *Brachythecium starkei*; Camso – *Campylium sommerfeltii*; Camst – *Campylium stellatum*; Cepbi – *Cephalozia bicuspidata*; Cepru – *Cephaloziella rubella*; Cerpu – *Ceratodon purpureus*; Cetis – *Cetraria islandica*; Cirpi – *Cirriphyllum piliferum*; Claar – *Cladonia arbuscula*; Claci – *Cladonia ciliata*; Clami – *Cladonia mitis*; Clapo – *Cladonia portentosa*; Clarn – *Cladonia rangiferina*; Clast – *Cladonia stellaris*; Clasy – *Cladonia stygia*; Claac – *Cladonia acuminata*; Claca – *Cladonia cariosa*; Clach – *Cladonia chlorophaea*; Claco – *Cladonia coniocraea*; Clacr – *Cladonia cryptochlorophaea*; Clafi – *Cladonia fimbriata*; Clafu – *Cladonia furcata*; Claoc – *Cladonia ochrochlora*; Clapy – *Cladonia pyxidata*; Clara – *Cladonia rangiformis*; Clare – *Cladonia rei*; Clasc – *Cladonia scabriuscula*; Clasq – *Cladonia squamosa*; Clasu – *Cladonia subulata*; Dicbo – *Dicranum bonjeanii*; Dicfl – *Dicranum flagellare*; Dicma – *Dicranum majus*; Dicpo – *Dicranum polysetum*; Dicsc – *Dicranum scoparium*; Dread – *Drepanocladus aduncus*; Euran – *Eurhynchium angustirete*; Eurpr – *Eurhynchium praelongum*; Eurpu – *Eurhynchium pulchellum*; Hylsp – *Hylocomium splendens*; Lopex – *Lophozia excisa*; Plaaf – *Plagiomnium affine*; Plame – *Plagiomnium medium*; Plala – *Plagiothecium laetum*; Plesc – *Pleurozium schreberi*; Pohnu – *Pohlia nutans*; Ptici – *Ptilidium ciliare*; Pticr – *Ptilium crista-castrensis*; Rhytr – *Rhytidiadelphus triquetrus*.

6. DISCUSSION

6.1 Ground vegetation

Dune woodlands are unique ecosystems with characteristic flora resulting from topographical and environmental heterogeneity. Although dune forests are considered to be a climax community of dune succession, long-term and short-term changes in species composition and richness occur over time (Provoost *et al*. 2011). In addition, changes in vegetation are affected by human activity (like exploitation of their natural resources, demographic expansion, recreation). Because of these constant natural and human induced changes, it is relevant to research and monitor the state of dune forests on a regular basis.

In total, 42 vascular plant, 43 bryophyte and 48 lichen species and subspecies were distinguished in the study area (**I**; **II**; **III**; **IV**). *Pleurozium schreberi* was the most abundant species, with a presence of 90% over all the quadrats, followed by *Vaccinium vitis-idaea* at 82%, *Vaccinium myrtillus* at 72%, *Deschampsia flexuosa* at 71%, *Melampyrum pratense* at 70% and *Hylocomium splendens* at 64% (**I**; **II**; **III**). Several species have been defined, according to the IUCN Red List categories, as being near threatened (NT), vulnerable (VU) or endangered (EN) in Estonia: *Festuca polesica* Zapal. (NT), *Lycopodium clavatum* L. (NT), *Cladonia portentosa* (Dufour) Follmann (NT) and *Cladonia scabriuscula* (Delise in Duby) Nyl. (VU). The species composition on the dunes studied is similar to both the lichen-rich *Pinus sylvestris* forest vegetation of the coniferous forest zone (Oksanen 1986) and the northern Swedish Boreal forest (Nilsson & Wardle 2005).

During dune succession, the vegetation typically undergoes changes that are similar the world over. On grey dunes, bryophytes and especially lichens are dominant, while in the next successional stage, as brown dunes, trees and dwarf shrubs prevail (Isermann 2011). During the initial phases of succession on nutrient-poor dune soils, different *Festuca* species are dominant, while *Deschampsia* replaces *Festuca* when soil accumulates a thicker organic layer (van Mierlo *et al*. 2000). In eight of the 232 quadrats in this study, *Festuca polesica* dominated; that *Deschampsia flexuosa* was dominant in 63 of the quadrats can be explained by the thick litter layer present in the study sites. In the current study, lichens were dominant in only seven of the quadrats on higher dunes in the bryophyte-lichen layer, and were poorly represented on lower dunes (**III**). Lichen species richness increases when different substrates are included (**IV**); when only terrestrial lichens are considered lichen species richness seems poor, but when epiphytic lichens are included species richness increases noticeably. Therefore, to estimate lichen species diversity different substrates should be investigated (Giordani & Brunialti 2015).

6.2 Environmental factors affecting ground vegetation

Ground vegetation zonation is typical for dunes and is observable on a larger scale (successional stages of dunes) as well as a smaller one (changes in species composition and horizontal structure of dunes) (Richards 1929; Zoladeski 1991; Isermann 2005; **I**; **II**; **III**; **IV**). Dune micro-topography is reported to be responsible for ground vegetation zonation on the Polish Baltic Sea coast (Zoladeski 1991). The results of the current study confirm ground vegetation zonation when all species are included: species that prefer a moister, more nutrient-rich habitat are found at the bottom of the dunes, while more xerophytic species are present on the top (**I**; **II**). On the slopes, only bryophyte and lichen layer species were identified as indicator species when all ground vegetation layers were studied together. In addition, most lichens were located on the southern and western slopes of the dunes (**III**). This appears to be because of the slope effect (gradient and aspect of slopes) — similar conclusions having been drawn by Jankowski (2010) and Sewerniak (2016) — suggesting that the slope aspect of dunes plays an important role in modifying local flora, by determining the amount of solar radiation that is received by the plants (Sigua *et al*. 2011). The results of the current study confirm the importance of aspect on the amount of solar radiation received, as PAR was significantly higher on the southern slopes of the dunes studied. According to Örd (1972a), slope inclination increases with height of the dune, especially in this particular dune system in south-west Estonia.

Dunes differ from each other according to their topographic features, and as a result microclimatic differences create different habitats. According to the results of the MRPP applied in this study, all the dunes differed from each other significantly in terms of ground vegetation species composition. Similar results were obtained by Hundt (1985), who found that dunes situated no more than 50 m from each other differed from each other considerably; Remke and Blindow (2011) too, found that despite their geographical closeness and comparable parent sand material, their study areas differed from each other considerably. However, when only vascular plants or bryophytes and lichens were analysed in the current study, lower dunes were not significantly different from each other in terms of species composition (**II**; **III**).

Soil type, which determines the forest site type typical of a forested area, is considered to be a very important environmental factor. The dominant soil type in forested inland dunes is Haplic Podzols, which are formed on the sand and characterised by low water-holding capacity and acidification (Örd 1972a; Örd 2000). Soil types in the current study varied according to dune profile. Similar results were described by Örd (1972a), who found that the thicknesses of different soil horizons also varied greatly (as indicated by the variation coefficient, by more than 30%).

Soils located on a lower position on dunes are characterised by more expressed effects of podsolization (Jankowski 2014). Podsolization is the main factor in soil development and Haplic Podzols are considered to be the climax of soil development under undisturbed *Pinus sylvestris*-dominated dune forests (Peyrat 2007). Köster and Kõlli (2013) found that several factors (like cutting, the age of stands but also stock density) can interfere with the assessment of soil type on the basis of ground vegetation. Successional soil development that becomes evident partly as nutrient mineralisation can cause shifts in species composition; this, in turn, appears to accelerate both an increase in nutrient mineralisation and changes in species composition during succession in nutrient-poor ecosystems (Berendse 1998). Based on the conclusions drawn by Örd (1972b), soil accumulates a litter layer extremely slowly, even when the soil has been covered with lichens and different species of *Poaceae* for decades. Elgersma (1998) suggested that organic matter is the main site factor that determines ground vegetation development.

The litter layer is considered to be the space or contact area for soil-plant interaction (Kõlli & Kanal 2010), while ground vegetation species composition depends on the properties of humus cover (Köster & Kõlli 2013). In northern coniferous forests, the soils are characterised by low rates of litter decomposition and slow decomposition promotes the accumulation of acid raw humus and the immobilisation of nutrients (Berg *et al*. 1987). According to Qian *et al*. (2003) many boreal plant species root directly in the humus layer and therefore thickness of litter layer plays great importance in dune areas. *Vaccinium myrtillus* and *V. vitis-idaea* have a strong positive effect on litter decomposition, while *Pleurozium schreberi* produces litter that decomposes slowly but accelerates the rate of vascular plant species litter decomposition (Wardle *et al*. 2003a; Nilsson & Wardle 2005). The dune area studied here showed quite similar results: the litter horizon was thicker under *Pleurozium schreberi*- and *Hylocomium splendens*-dominated bryophyte-lichen communities; while among vascular plant species, *Convallaria majalis* and *Maianthemum bifolium* were dominant in quadrats with a thicker litter horizon. The results suggest that the composition of bryophyte and lichen communities is strongly affected by the thickness of a moderately decomposed litter layer (**III**) and that the litter layer is thinnest on lichen-dominated quadrats. These results are in accordance with those of Màrialigeti *et al.* (2009) suggesting that litter cover affects mainly bryophyte assemblages. It is assumed that the soil organic layer is thick under *Empetrum nigrum*-dominated areas (Tybirk *et al*. 2000; Nilsson & Wardle 2005), and the results of the current study confirm that *Empetrum nigrum*–*Pleurozium schreberi*- and *Empetrum nigrum*–*Hylocomium splendens*-

dominated quadrats showed the highest average litter layer thickness.

Podzols on fixed dunes are usually strongly to moderately acidic (Örd 1972b; **I**; **II**; **III**; **IV**). The process of soil acidification is related to the accumulation of organic matter (Berendse 1998), with acidification increasing with successional age (Peyrat 2007; Lane *et al*. 2008). Giesler *et al*. (1998) found that in Boreal forests the soil pH and supply of base cations were connected to plant cover productivity and composition. Isermann (2005) found that with higher soil pH variability, species diversity increased. According to the current results for higher dunes, soil pH varied by more than three units (from 3.4 to 6.6) and resulted in higher species richness compared with lower dunes whose soil pH varied by just under 1.8 units. Such high variability of soil pH on dunes can be partly explained by destructive human activity caused erosion due to which loose sand and litter free wide trails occur. Brunbjerg *et al*. (2015) found that soil pH varied from 3.8 to 6.9 on dune areas with different kind of physical disturbance types. Areas with loose sand are considered more suitable for some lichens, which can act as pioneers and avoid competition with vascular plant species (Ketner-Oostra & Sýkora 2000). The results in **I** are consistent with the results presented in paper **II** where soil pH was found to be an important factor for vascular plants species richness and cover, while the effect of pH on vascular plant species composition appeared to be smaller according to the NMDS ordination. According to the results of Gheza *et al*. (2015), terrestrial bryophytes and lichens are mainly acidophytic. For bryophytes and lichens, soil pH is considered to be an important factor affecting species composition in the bryophyte-lichen layer (**III**), although in paper **IV** soil pH showed no relationship with bryophyte and lichen species diversity; this may be explained by differences in the sampling methodology and the depth at which soil samples were taken. Dune soils are supposed to be enriched with water soluble salts (Corwin & Lesch 2005), but the average salt content of soil-water suspensions at different zones were not salty or nearly not salty, staying below 0.75 dS m^{-1} (classification value suggested by FAO (2006)). Therefore, soil salinity does not hinder plant growth on the studied dune area, but at the same time, such low values of soil electrical conductivity suggest that the soils are suffering under nutrient deficiency.

Soil fertility on dunes depends on many factors, such as the zone on the dune, slope aspect or soil moisture. The current study indicated that N, P, K, Ca and Mg content in dune soils was positively correlated with soil moisture values. Similar observations have been made by Sewerniak *et al*. (2017), who found that lower-situated dune soils with high moisture values were characterised by higher fertility. Northern slopes are much more fertile compared with southern slopes (Sigua *et al*. 2011; Huang *et al*. 2015).

According to Lichter (1998), plant growth on forested dunes is limited by K and P content, whereas Ca and Mg contents are less relevant. These results are not fully in accordance with those of the current study, which showed ground vegetation species richness and composition to be partly determined by K and Ca content (Figure 4, Table 5 and 6 in **II**; Figure 5 and Table 5 in **III**; Figure 10 and Table 8 in the current thesis). Conclusions drawn by Chandapillai (1970) suggest that vegetation has lower cover values because of lower levels of N and K. According to results based on vascular plant species data, total coverage of vascular plant species is lower in the case of higher total N content, while a higher K content increases vascular plant species coverage. Lower cover values related to higher nitrogen contents can be explained by higher abundance of grasses (species of *Festuca* and *Deschampsia*) which have lower cover values.

Increased N-deposition is considered to be responsible for grass encroachment on acidic dunes (Kooijman *et al*. 2017). In the current study, a higher N value decreased vascular plant species richness in the dunes studied; similar results have been reported by Kooijman *et al*. (2017). Lichter (1998) found that species diversity was highest on dunes where no environmental resource shows extremely low or high values. The studied areas should be further investigated for N, because increased N loads in acidic systems probably result in a decrease in species richness and change in vegetation (Remke *et al*. 2009; Provoost *et al*. 2011; Kooijman *et al*. 2017). Although Estonia reached the required nitrogen atmospheric emission levels already in 2010 (HELCOM 2015), the large proportion of airborne nitrogen deposition is classified as transboundary and the atmospheric deposition of total nitrogen is strongly affected by climatic conditions and variations of meteorological conditions such as direction of dominating winds, precipitation etc. (Bartnicki *et al*. 2017).

Light limitation is an especially important environmental factor for open-dune species adapted to high light availability (Lichter 1998). In later successional stages, when dunes become fixed with trees, canopy cover values appear to be a major factor affecting bryophyte and lichen species composition and richness (**III**); Kershaw (1977) postulated that greater tree canopy cover causes lichen-rich stand development in *Pleurozium schreberi*-dominated stands. It could be said that vascular plant species richness, cover and composition are also significantly affected by light conditions; a higher amount of light reduces vascular plant species richness allowing cryptogams to inhabit these areas. Because of the extreme growth conditions on the slopes, lichens were the only life-forms, besides *Ceratodon purpureus*, recorded as an indicator species on the slopes of the dunes when all taxonomic groups of ground vegetation were taken into account. This is in accordance with Oksanen (1983) and Sewerniak (2011), who found that in the northern hemisphere lichen-dominated patches prefer south-facing slopes, which receive more solar radiation and therefore have more extreme growth conditions (higher soil temperature, less soil moisture and nutrient-poor soil) resulting in lower vascular plant species cover. Furthermore, dune slopes are more open to wind-related activities, which in turn dry the soils further (Sewerniak 2011).

Soil moisture is thought to be one of the main factors that limit plant growth on fixed dunes (Niu *et al*. 2005). The current results support this view, as ground vegetation species richness, cover and composition were related to average soil moisture content (**I**; **II**; **III**). Soil moisture was related to the zone, aspect and relative height of dunes (**I**; **II**; **III**). Typically, soil moisture and elevation are not related in a monotonic way (Solon *et al*. 2007) but are modified by slope steepness and micro-topographic conditions (Shary *et al*. 2002). It is known that *Empetrum nigrum* prefers moist plateaus and the northern slopes of higher dunes, while *Vaccinium myrtillus* is typical of mesic areas of dunes and *V. vitis-idaea* common in dry sites (Ujházy *et al*. 2011). Hundt (1985) and Örd (1972a) found that humus and litter layers on both grey and brown dunes were correlated with higher soil water content. The results of this study showed no such relationships between differently decomposed litter layers and soil water content in different seasons. It is recognised that soil moisture values in the upper soil layer of dune areas are extremely low during the vegetation period, often lower than 5%, and highly dependent on rainfall (Wilde 1958).

Forest ecosystems on dunes form for nearly 300 years (Lichter 1998) and are considered very fragile ecosystems, especially lichen-rich stands (Kutiel *et al*. 1999, 2000; Lemauviel *et al*. 2003; Van Der Maarel 2003). Therefore, every decision made concerning these habitats should be contemplated carefully. Human-induced disturbances such as urbanisation and recreation are on the rise in these habitats and consequently more degraded areas are expected to appear (European Commission 2016).

6.3 Ecosystem services and forestry aspects

Ground vegetation in dune forests provides multiple ecosystem services for humans, from picking berries and mushrooms to ecotherapy and recreation. It also controls natural forest regeneration, creates a habitat for wildlife and regulates forest nutrient cycling (Berendse 1998; Nilsson & Wardle 2005; Kohv 2012). The social values of ecosystem services have been defined by van Riper *et al*. (2012) as 'the perceived qualities carried by a natural environment that provides benefits to support human wellbeing'. According to the conclusions of Everard *et al*. (2010), the societal value attributed to sand dunes (the social value of the ecosystem services that dunes provide) and their associated protective measures are not sufficient. Hence, conservation measures are focused primarily on biodiversity and its protection, ignoring the need to care for the wider range of ecosystem services provided by dunes (Everard *et al*. 2010; Barbier *et al*. 2011).

Over time, dunes, their shape and their plant species composition have been changed and altered by urban development and recreational activities. In some cases, such disturbance has been found to increase species richness (Brunbjerg *et al*. 2015). Nevertheless, where ground vegetation is concerned, pedestrian trampling, vehicular traffic and various recreational activities are considered to be most destructive (Kutiel *et al*. 2000; Grunewald 2006); similar issues have been reported in the study areas, especially in relation to all-terrain vehicles (ATV) and off-road motorcycles (UPMP 2016; LPMP 2017). Although the areas studied are under protection, there are no restrictions on pedestrians; and while vehicles are not allowed to be driven beside trails and roads, inadequate supervision means that large areas contain illegal footpaths and vehicle roads where the ground vegetation or soil has been damaged. To protect the fragile ground vegetation layer and continue to provide various ecosystem services for humans, various approaches could be adopted. For example, where pedestrian trails are concerned those with high visitor use should be preferred over more numerous low-use ones; Kutiel *et al*. (1999) found that the spatial damage caused by numerous low-use trails was higher compared with that incurred by trails with high visitor use.

For forestry, ground vegetation importance is its influence on the growth and development of tree seedlings. According to Coomes and Grubb (2000), on infertile and dry soils pine seedling growth in forests is limited by competition for below-ground resources. Similar results were obtained by Axelsson *et al*. (2014). The unsatisfactory natural regeneration of pine in dune forests was noted as far back as the 1930s by Rühl (1932), while according to Örd (2000) the natural regeneration of pine was absent in 81% of the 100-year-old and older pine forests he studied. According to previous works done in studied area by Kõresaar *et al*. (2008), the number of natural regeneration trees on site 1 was 3,867 trees per ha, on site 2 3,000 trees per ha, on site 3 1,861 trees per ha and on site 4 2,733 trees per ha. Kõresaar (2003) found that stand relative density in the *Cladonia* forest site type in the range

0.45–0.88 did not influence the number of natural regeneration of trees, while on the *Rhodococcum* forest site type a relative density of 0.40–0.73 showed a strong negative effect on the number of second-growth pine trees. Hale *et al*. (2009) found that in Britain, a Scots pine stand required a basal area of less than 27 m^2 ha^{-1} to achieve transmittance suitable for the growth of Scots pine seedlings. According to measurements conducted in 2012 by the Estonian State Forest Management Centre on site 1 of the current study, the average stand basal area was 19.4 m^2 h^{-1}, on site 2 16.0 m^2 h^{-1}, on site 3 21.5 m^2 h^{-1} and on site 4 16.2 m^2 h^{-1}. It is known that some ground vegetation layer species can inhibit tree seed germination and seedling growth. On sites where black crowberry (*Empetrum nigrum*) is dominant in the ground vegetation layer, tree seed germination and seedling growth has been found to be reduced (Nilsson *et al*. 2000; Wardle *et al*. 2003b). On relatively lower dunes, where the bryophyte layer is comparatively homogeneous, ground vegetation layer is not so fragile compared with that on higher dunes where lichen-rich patches occur. Steijlen *et al*. (1995) found that seedlings planted in a dense feather moss (*Pleurozium schreberi*, *Hylocomium splendens*, *Ptilium crista-castrensis*) layer showed scanty growth.

In protected areas, cutting must be carried out in accordance with the Nature Conservation Act (2004) and protection management plans for the area (LPMP 2017; UPMP 2016). The aim of cutting is not for economic benefits but for protection purposes. The dune forests in the area studied are part of the Luitemaa nature reserve and Uulu-Võiste landscape protection area and are therefore protected forests (Nature Conservation Act 2004; LNRPR 2006; ULPFPR 2016).

These pine forests have been managed for a century through uniform shelterwood cutting or selection cutting (Örd 2000). The valid Forest Act (2006) offers the option of using formative cutting in order to meet protection goals in accordance with protection management plans and action plans for the protection and control of species, or for the purpose of preserving and improving the status of a protected individual natural object or key habitat.

When the purpose of the cutting is not to create ground vegetation-free sandy patches (which are important for the reproduction or survival of some species, like the sand lizard *Lacerta agilis*), then it should be performed carefully so as not to destroy the ground vegetation layer. Uniform shelterwood cutting or formative cutting should be preferred on the bottoms and tops of the dunes to ensure sufficient shelter for the undergrowth, while the soil and ground vegetation layer offers suitable conditions for undergrowth formation. In areas where *Empetrum nigrum* or feather mosses create thick mattes, scarification or mechanical disturbance of the ground vegetation layer might be needed (Örd 1972a; Kõresaar 2003) because these species are known for inhibiting seed germination and seedling growth (Tybirk *et al*. 2000; Nilsson & Wardle 2005).

When the aim of the cutting is to create sandy patches on the slopes of the dunes, then group selection cutting should be preferred on the southern and western slopes of the higher dunes. This is necessary to create patches free from shade and, with the increased impact of sun and wind over time, for a lichen-rich community to occur. Lichen species richness is considered to be a time-related phenomenon on fixed sand dunes (Ketner-Oostra & Sykora 2000). Attention should be paid to areas in which *Calluna vulgaris* is abundant nearby because, according to Örd (1972a), *C*. *vulgaris* may inhabit these sandy patches before lichens can. The purpose of forest management in protected areas is to protect nature and its biological diversity hence there are no definitive rules for forest management.

7. CONCLUSIONS

One hundred and thirty-three ground vegetation species were recorded on five dunes of differing heights in the south-west Estonian dune area (**I**; **II**; **III**; **IV**): 42 vascular plant, 43 bryophyte and 48 lichen species were identified.

Ground vegetation species richness and species' horizontal and vertical structure on forested dunes are highly dependent on topography-induced differences in the site, aspect, height and zone of the dunes (**I**; **II**; **III**; **IV**). The environmental factors that control ground vegetation, species richness and composition in a fixed dune landscape are different for vascular plant species, bryophytes and lichens.

The first hypothesis of this thesis was partially confirmed because ground vegetation zonation was present on all five dunes; however, regardless of the height of the dune, ground vegetation zonation was observed when different taxonomic groups (vascular plants, bryophytes, lichens) were included. When only vascular plant species composition was analysed for all dunes, communities from the bottoms of the dunes had a distinctively different species composition compared with those from the tops and slopes (**II**). Bryophyte and lichen communities on the tops of the dunes differed significantly compared with those on the slopes and bottoms, while species composition on the slopes and at the bottoms were similar (**III**). On the basis of vascular plant species and bryophyte-lichen species richness and composition, the lower dunes showed no statistically important differences compared to each other (**II**; **III**); however, when dunes were compared on the basis of ground vegetation species richness and composition, all sites differed from each other considerably.

As predicted by the second hypothesis, vascular plant species richness was affected by various environmental factors including soil pH and soil moisture. The most important of the factors controlling the complex of ground vegetation studied were light conditions (PAR and canopy cover), soil water content, thickness of the moderately decomposed litter layer and potassium and calcium content in the soil (**I**; **II**; **III**). Vascular plant species richness and composition on forested dunes was also dependent on the absolute height of the dune, its zone and aspect, soil nitrogen, potassium and phosphorus content, the cover of the bryophyte-lichen layer and light conditions (**II**). When the amount of light and content of nitrogen increased, vascular plant species richness showed a significant decrease (**II**), therefore it can be concluded that soil higher nitrogen content decreases vascular plant species richness on forested sand dunes in South-west Estonia.

Regarding bryophyte and lichen layer species composition, the most important factors were the height, aspect and zone of the dune, light conditions, soil pH and electrical conductivity, soil water content, vascular plant species cover and thickness of the moderately decomposed litter horizon (**III**). Lichen species richness was highest on the slopes of the dunes, where the cover of vascular plant species was lowest, while bryophyte species richness was higher at the bottoms and decreased towards the tops of the dunes (**III**).

Ground vegetation species richness and composition on the forested dunes studied in the Uulu-Rannametsa area were found not to be controlled by one or two factors but rather by a complicated system of environmental variables that showed distinct effects on different ground vegetation life-forms. Environmental and topographical factors that affect the formation of ground vegetation are strongly related to the successional stage of the dune and the soils and forest on it. The current thesis provides new and statistically relevant information about fine-scale variations in ground vegetation communities and their relationships to various environmental conditions on *Pinus sylvestris*-dominated inland dunes causing ground vegetation zonation on the dunes. The results of this thesis also suggest that every dune site is unique and that the management policy should take into account this specificity.

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SUMMARY IN ESTONIAN

ALUSTAIMESTIKU MITMEKESISUS JA GEOBOTAANILINE ANALÜÜS EDELA-EESTI LUITEMÄNNIKUTES

Sissejuhatus

Boreaalse piirkonna metsastunud luited (elupaigatüüp 2180) kuuluvad Euroopa Liidu Nõukogu loodusdirektiivi lisa I (1992) kohaselt esmatähtsate elupaigatüüpide loetellu. Viimaste seireandmete põhjal hinnati mainitud elupaigatüüp haavatavaks ja nende alade kaitse ebapiisavaks (European Commission 2015, European Commission 2016). Jaapanis Nagoyas võeti bioloogilise mitmekesisuse konventsiooni kümnendal konverentsil 2010. aastal vastu ülemaailmne elurikkuse strateegia aastani 2020 ja visioon aastani 2050. Riigid leppisid kokku üldeesmärgis – elurikkuse kao peatamiseks tuleb tegutseda efektiivselt ja kohe tagamaks, et 2020. aastal toimivad ökosüsteemid endiselt, pakkudes olulisi teenuseid, hoides planeedil mitmekesist elu ning panustades inimese heaolusse ja vaesuse vähendamisse (Conference of the Parties 2010). Eestis on luitemaastiku pindala suurus ligikaudu 200 ruutkilomeetrit, millest metsastunud luidete elupaigatüüp moodustab enamuse (Ratas jt 2008).

Metsastunud luideteks loetakse looduslike või poollooduslike puistutega kaetud luiteid (European Comission 2013). Edela-Eesti rannikumaastikule on iseloomulikud Antsülusjärve ja Litoriinamere transgressioonil tekkinud liivaluited, mis on aja jooksul kinnistunud ning kaetud männimetsadega (Ratas ja Rivis 2003). Uulu ja Rannametsa vahele jäävad luitemetsad on juba sajandeid kaitse alla kuulunud. Esimesed teated pärinevad 1786. aastast, kui ala valitsejad võtsid vastu seaduse vanade luitemetsade kaitseks. Aastatel 1839 ja 1888 võeti piirkonna luitemetsad maastikukaitse eesmärgil kaitse alla (Örd 2000, Meikar 2001, Kose jt 2003). Kaitsealused metsad kuulusid Häädemeeste (*Gudmannsbach*) ja Tahkuranna (*Tackerort*) riigimõisate alla (Tammekann jt 1930). 1958. aastal moodustati

Rannametsa luidete, Tolkuse raba, Timmkanali paljandi jms loodusväärtuste kaitseks looduskaitseala, millele liideti 1976. aastal põhja poole jäävad alad (Kose jt 2003, LPMP 2017). Aastal 1991 moodustati Rannametsa-Soometsa looduskaitseala, mis 2006. aastal hakkas kandma Luitemaa looduskaitseala nime (Kose jt 2003). Uulu-Võiste maastikukaitseala loodi 2016. aastal Uulu-Võiste hoiuala, Surju rannametsade kaitseala ja Uulu-Võiste loodusala baasil (UPMP 2016). Luitemaa looduskaitseala kogupindala on 11 301 ha ning Uulu-Võiste maastikukaitseala hõlmab 690 ha (UPMP 2016, LPMP 2017). Rannametsas asuvad Eesti kõrgeimad luited, Tornimägi (34 m) ja Tõotusemägi (32 m).

Kuigi luitemetsade puistu on koosseisult enamasti ühevanuseline (enamasti puhtmännik) (Pärn 2003, Peyrat 2007), võib alustaimestik liigiliselt koosseisult väga palju varieeruda. Üheks liigirikkuse ja liigilise mitmekesisuse põhjuseks peetakse kasvutingimuste heterogeensust (Pausas ja Austin 2001, Bartels ja Chen 2010), samas Huston (1979) on leidnud, et liigirikkus luidetel sõltub kahest universaalsest tegurist – häiringute intensiivsusest ja mulla viljakusest. Nylen ja Luoto (2015) lisavad eelnimetatutele veel luite suktsessiooni staadiumi.

On teada, et taimestik moodustab erinevaid tsoone sõltuvalt luite vanusest, kinnistumise astmest ja suktsessiooni staadiumist. Erinevate tsoonide eristamiseks tuleb liikuda ranniku taimestumata lahtistelt luidetelt sisemaal paiknevate metsastunud luideteni (Baldwin ja Maun 1983, Lane jt 2008). Vähem on teavet tsonaalsuse kohta ühe luite piires ja tsonaalsust põhjustavate keskkonnatingimuste kohta (Zoladeski 1991, Ujházy jt 2011).

Asukohta reljeefil peetakse üheks tähtsamaks teguriks, mis määrab ära mullatekke protsessi intensiivsuse, alustaimestiku kujunemise ja liigilise koosseisu (Jenny 1941, Zoladeski 1991, Peyrat 2011, Soil Science Division Staff 2017). Eltermann ja Raukas (1966) on selgitanud, et Rannametsa piirkonna luited on ebatüüpilised: nii mere- kui ka maismaapoolsed luitenõlvad on suhteliselt järsud (25–45°), tekitades erinevate tingimustega kasvukohti, mistõttu võib luitel esineda mitu metsakasvukohatüüpi: mustika, pohla, sambliku ja kanarbiku metsakasvukohatüübid (Örd 1973, Mandre ja Korsjukov 2003, Pärn 2003). Luidete vanus ja suktsessiooni staadium mõjutavad luidetel esinevate liikide mitmekesisust (Isermann 2011). Luitemetsa peetakse luidete suktsessiooni viimaseks staadiumiks, kusjuures metsa looduslik kujunemine luidetele võib võtta aega ligikaudu 300 aastat (Lichter 1998). Samblike suur liigirikkus kinnistunud luidetel on ajaliselt piiratud. Taimkatte arenguga kaasnevad muutused mulla omadustes, mistõttu asenduvad vähese konkurentsivõimega samblikud suktsessiooni käigus sammalde ja soontaimeliikidega (Ketner-Oostra ja Sykora 2000, Ketner-Oostra jt 2010).

Luitemetsade mullad on enamasti erineva leetumisastmega leedemullad (Haplic Podzol) (Örd 1972a, Peyrat 2007, Mandre jt 2008), kus huumushorisont esineb põhiliselt õhukese kihina luidete jalamitel (Mandre jt 2008). Peyrat (2007) on leidnud, et leedemullad on iseloomulikud häiringuteta luitemetsadele mullaarengu kliimaksstaadiumis. Luitemetsade mullad on keskmiselt kuni tugevalt happelised (Örd 1972, Isermann 2005, Mandre jt 2008) ning mulla pH ja veemahutavus on tähtsad tegurid, mis määravad liigirikkuse ruumilise paiknemise (Schaffers 2002). Luitealasid peetakse väga kuivadeks ökosüsteemideks (Chandapillai 1970, Van der Maarel 1993), kus muldade väike veemahutavus piirab taimede füsioloogilisi protsesse (Niu jt 2005). Kõduhorisondi tüsedus mõjutab mulla veemahutavuse võimet (Berendse 1998, Elgersma 1998, Sewerniak jt 2017). Luitemetsade alustaimestiku varieeruvust võivad põhjustada ka muutused mulla toitainete sisalduses (Lane jt 2008). Eriti oluliseks peetakse mulla lämmastikusisaldust, mille suurenev depositsioon põhjustab luitealadel alustaimestiku liigirikkuse kadu (Provoost jt 2011, Kooijman jt 2017). Boreaalse vööndi luitemuldade geneesi käigus toimub toitainete mineraliseerumine ja orgaanilise aine kogunemine, mulla pH muutub happelisemaks, kaltsiumisisaldus väheneb ning aja jooksul liigid vahelduvad (Peyrat 2007, Berendse 1998).

Luitemetsade valgustingimused on seotud luitemetsa puistu arengujärguga ning alustaimestiku areng, mitmekesisus ja struktuur sõltuvad maapinnale jõudva päikesevalguse hulgast (Bartels ja Chen 2010). On teada, et luitemetsades leidub samblikurikkaid alasid lõunapoolsetel kuivadel ja päikesepaistelistel nõlvadel, samas kui samblad eelistavad põhjapoolsemaid niiskemaid ja varjulisemaid alasid (Oksanen 1983, Sewerniak 2016).

Taimestikku peetakse luidete stabiilsuse tagamisel üheks tähtsamaks teguriks (Provoost jt 2011). Luitemets ei teki kunagi lahtistele luidetele, enne on vajalik huumuskihi teke (Ilves 1966). Liigilise mitmekesisuse uuringud ning luitemetsades elurikkust määravate keskkonnatingimuste kindlakstegemine võimaldab nende alade säilitamiseks, kaitsmiseks ja majandamiseks teha paremaid otsuseid. Doktoritöö eesmärk oli uurida luitemetsade alustaimestiku liigilist mitmekesisust ja leida, millised keskkonnatunnused mõjutavad soontaimede, sammalde ning samblike liigirikkust ja liigilist koosseisu luitemetsades. Eelnevast lähtudes seati järgmised alameesmärgid ja hüpoteesid:

- Selgitada ja analüüsida millised prooviala asukoha, mulla ja valgustingimustega seotud tunnused mõjutavad alustaimestiku liigilist mitmekesisust Edela-Eesti luitemännikutes (**I**, **II**, **III**);

- Tuvastada alustaimestiku liigilise koosseisu tsonaalsus mööda luite kõrgusgradienti (**I**, **II**, **III**, **IV**). Hüpoteesiks seati, et luidete jalamil, keskosal ja harjal on liikide koosseisu erinevus statistiliselt oluline, eristuvad luidete jalamile, keskosale ja harjale iseloomulikud kooslused ning need eristuvad selgelt ainult kõrgemaks määratletud luidetel (**I**, **II**, **III**, **IV**);

- Analüüsida soontaimede liigirikkust metsaga kaetud luidetel (**I**, **II**). Eeldati, et soontaimede liigirikkus ja liigiline koosseis sõltuvad kuivadel ning toitainevaestel muldadel peamiselt mulla omadustest ja kasvukoha valgustingimustest ning soontaimede liigirikkus väheneb mullas sisalduva lämmastikuhulga suurenemisel (**I**, **II**);

- Analüüsida sammalde ja samblike liigirikkust luitemännikutes (**III**, **IV**). Sammalde ja samblike liigirikkuse ning liigilise koosseisu uurimisel oletati, et koosluse struktuuri mõjutab enim mulla veesidumisvõime ja mulla pH ning samblike liigirikkus suureneb aladel, kus soontaimede katvus on madalam (**III**, **IV**).

Materjal ja metoodika

Luitemetsade alustaimestiku liigilise mitmekesisuse ja liigirikkuse uurimiseks valiti Edela-Eestis Uulu ning Häädemeeste vahele jäävalt alalt viis tüüpilist luidet, mille kaugus rannajoonest on ligikaudu 2–3 km. Alad 1, 2 ja 5 paiknevad Luitemaa looduskaitsealal ning kuuluvad kõrgemate luidete hulka. Luitemaa looduskaitsealal on kaitsealused elupaigatüübid järgmised: *2130 (rohttaimedega kinnistunud rannikuluited (hallid luited), 2180 (atlantilise, kontinentaalse ja boreaalse piirkonna metsastunud luited), 2190 (niisked luitenõod). Madalamate luidete alad 3 ja 4 asuvad Uulu-Võiste maastikukaitsealal, kus kaitstavad elupaigatüübid on *9010 (vanad loodusmetsad), 9080 (Fennoskandia soostuvad ja soo-lehtmetsad), 2180 (atlantilise, kontinentaalse ning boreaalse piirkonna metsastunud luited).

Proovialade täpne asukoht ja iga prooviruudu kõrgus mõõdeti Garmin GPSMap 76CSx tasku-GPS-navigaatoriga. Puistut iseloomustavad takseernäitajad saadi Riigimetsa Majandamise Keskuse andmebaasist ning Kõresaare (2003), Pärna (2003), Kõresaare jt (2008) töödest. Uuringuala metsad on enamasti loodusliku tekkega (83,8%) puhtmännikud (Pärn 2003). Piirkonna luitemännikutele on iseloomulik kõrge vanus (120—190 aastat) ja ebapiisav looduslik metsauuendus (Örd 1972a, Kõresaar 2003, Pärn 2003). Piirkonna sademete ja temperatuuride andmed uuringuperioodide kohta pärinevad Riigi Ilmateenistuse Pärnu seirejaama andmebaasist.

Luidete topograafilistest näitajatest määrati iga prooviruudu koordinaadid, kõrgus merepinnast (m), suhteline kõrgus (m), kaldenurk (°), suund ilmakaarte suhtes ja asukoht luitel (jalam, keskosa, hari). Mulla iseloomustamiseks määrati mullaliigid luidete jalamitel, keskosal ja harjal, hinnati mullahorisontide tüsedust (cm) ning võeti analüüsid mulla pH, elektrijuhtivuse ja põhitoitainete (N, P, K, Ca, Mg) sisalduse määramiseks laboritingimustes.

Kasvuperioodi vältel (kevadine, suvine ja sügisene sisaldus) mõõdeti mullas sisalduva vee hulga (%) väärtused (Field Scout™ TDR 300) eeltingimusel, et kolm päeva varem ei ole vihma sadanud. Valgustingimuste hindamiseks mõõdeti 2008. aastal 23. juuli keskpäeval lühikese aja jooksul alustaimestikuni jõudva fotosünteetiliselt aktiivse kiirguse hulk iga ruudu kohta (Decagon Devices AccuPAR Model PAR-80, $\mu mol\, m^{-2}s^{-1}$). Lisaks määrati visuaalse hindamise teel igal ruudul puistu võrastiku liituvus, hinnates puuvõradega kaetud pinna suurust prooviruudul. Tulemus väljendati skaalal 0–1 (Masing 1979, Pihelgas 1983).

Soontaimede, sammalde ja samblike liigilise koosseisu ning horisontaalse struktuuri määramiseks rajati kokku 251 ühe ruutmeetri suurust prooviruutu (**I**, **II**, **III**). Prooviruudud paiknesid aladel 1, 2, 3 ja 4 sirge transektina üle luiteharja ning prooviruutude vahe oli üks meeter (**II**, **III**). Alal 5 paiknesid transekt ja prooviruudud läänepoolsel luitenõlval vahega üks meeter (**I**, **IV**). Prooviruutudel määrati soontaimede, sammalde ja samblike üldkatvus, seal esinevad liigid ning nende katvus, soontaimede puhul määrati veel ka ohtrus.

Sambla-, sambliku- ja soontaimeliikide liigirohkust (S) hinnati liikide koguarvuna iga ruudu kohta. Lisaks arvutati iga ruudu kohta Simpsoni mitmekesisusindeksid (D'). Kochi indeksit (K_K) kasutati soontaimede koosluste homogeensuse hindamisel erinevatel luidetel ja Sørensoni sarnasuskoefitsienti (K_S) kasutati soontaimede koosluste sarnasuse hindamisel erineva kõrgusega luidetel.

Andmeanalüüsi käigus kasutati regressioon- ja korrelatsioonanalüüsi tegemiseks andmetöötlusprogramme MS Excel 2003, MS Excel 2010 ja Statgraphics (**I**, **II**, **III**, **IV**). Statistikaprogrammi PC-ORD versiooni 6 kasutati mitmese reaktsiooni permutatsiooni protseduuri (MRPP), indikaatorliikide analüüsi (ISA) ning kooslust iseloomustavate indeksite arvutamisel (**II**, **III**). Vabavaralise statistikaprogrammi R Statistics versiooni 3.2.3 pakettide „lme4“ ja „Vegan“ abil tehti kogutud andmete mitteparameetriline ordinatsioonanalüüs (NMDS) ning analüüsiti andmeid lineaarse segamudeli abil (**II, III**).

Tulemused ja järeldused

Alustaimestiku liigirikkuse uurimisel tuvastati 42 soontaimeliiki, 43 samblaliiki ja 48 samblikuliiki (**I**, **II**, **III**, **IV**). Harilik palusammal (*Pleurozium schreberi*) oli levinuim liik, esinedes 90%-l ruutudest, sellele järgnesid harilik pohl (*Vaccinium vitis-idaea*) 82%-l, harilik mustikas (*Vaccinium myrtillus*) 72%-l, võnk-kastevars (*Deschampsia flexuosa*) 71%-l, palu-härghein (*Melampyrum pratense*) 70%-l ja harilik laanik (*Hylocomium splendens*) 64%-l ruutudest. Rahvusvahelise Looduskaitseliidu (IUCN) punasesse nimistusse kantud ohustatud liikidest esinevad alal liiv-aruhein *Festuca polesica* (ohulähedane), karukold *Lycopodium clavatum* (ohulähedane), sagris põdrasamblik *Cladonia portentosa* (ohulähedane) ja kare porosamblik *Cladonia scabriuscula* (ohualdis). Uuritud luitemetsade puistu keskmine vanus on hinnanguliselt 200 aastat, samas Eestis on männikute keskmine vanus 73 aastat. Männipuistud vanusega 121 aastat ja enam moodustavad 6% kõigist männipuistutest (Environment Agency 2016).

Luidete vanus ja suktsessiooni staadium on väga tähtsad tegurid, mis määravad ära luidetel esinevate liikide hulga ning koosluste liigilise koosseisu. Luidete suktsessiooni käigus taimestik muutub, hallidel taimestunud luidetel domineerivad samblad ja samblikud, samas kui järgmises staadiumis, s.t pruunidel luidetel domineerivad puud ja kääbuspõõsad (Isermann 2011). Kõrgematel luidetel domineerisid samblad ja samblikud ainult seitsmel ruudul ning olid vähe esindatud madalamatel luidetel (**III**). Sammalde ja samblike liigirikkus oleks olnud märgatavalt suurem, kui uuringusse oleks kaasatud ka epifüütsed liigid (**IV**).

Alustaimestiku tsonaalsus on luidetele iseloomulik ning väljendus liigilise koosseisu muutustes uuritud luidetel, sõltudes asukohast luitel ja analüüsitud taksonoomilistest gruppidest (**I, II**, **III**, **IV**). Indikaatorliikide analüüs tõi välja luidete jalamile, keskosale ja harjale iseloomulikud alustaimestiku liigid. Seejuures on indikaatorliikide arv luidete keskosas väikseim ning liigid kuuluvad sammalde ja samblike hulka. Luite jalamil esinevad niiskemaid ja toitainerikkamaid kasvukohti eelistavad liigid, samas kui luite harjale on iseloomulikud liigid, kes taluvad kuivust ja toitainevaegust (**I**, **II**). Töös leidis kinnitust hüpotees, et luitemetsade alustaimestik moodustab luidete jalamitele, keskosale ja harjale iseloomulikke kooslusi (**I**, **II**, **III**, **IV**). Osaliselt ei leidnud kinnitust hüpotees, et tsonaalsus on iseloomulik ainult kõrgematele luidetele. Kui esialgses väiksema valimiga uuringus (**I**) selgus, et ainult kõrgemal luitel moodustab alustaimestik sõltuvalt asukohast tsoone, siis järgnevad suuremale valimile tuginevad uuringud lükkasid selle ümber (**II**, **III**).

Tegurid, mis mõjutavad alustaimestiku liigirikkust ja koosluse liigilist koosseisu metsastunud luidetel, on soontaimedel, sammaldel ning samblikel erinevad. Soontaimede liigirikkust ja liikide mitmekesisust luidetel on enim mõjutanud luite topograafilised omadused, nagu luite absoluutne kõrgus, asukoht luitel ja paiknemine ilmakaarte suhtes, samuti substraadi pH, lämmastiku-, fosfori- ja kaaliumisisaldus, mullaniiskus ning valgustingimused (**II**). Soontaimede puhul on oluline näitaja ka sambla- ja samblikurinde üldkatvus (**II**). Luitemetsade soontaimede liigirikkus väheneb märgatavalt suurenenud lämmastikuhulga korral (**II**).

Sambla- ja samblikurinde liigilist koosseisu ning struktuuri määravad luite kõrgus, paiknemine ilmakaarte suhtes, asukoht luitel, lisaks valgustingimused, mulla pH, lahustuvate soolade ioonide kontsentratsioon mullalahuses, mullaniiskus, soontaimede katvus ja mõõdukalt lagunenud kõdukihi tüsedus (**III**). Need tulemused kinnitavad hüpoteesi, mille kohaselt mõjutab sammalde ja samblike kooslusi mullaniiskus ja pH. Kui sammalde liigirikkus püsis kogu luite piires suhteliselt stabiilsena, olles suurim luidete jalamitel, siis samblike liigirikkus oli suurim luidete nõlvadel, kus maapinnale jõudvat valgust oli kõige enam, mullaniiskus ja soontaimede katvus väikseim (**III**).

Analüüsides uuritud luitemetsade alustaimestikku tervikuna ja koosluse liigilist koosseisu mõjutavaid tegureid, ilmnes, et statistiliselt olulised on luite kõrgus ja paiknemine ilmakaarte suhtes, mõõdukalt lagunenud kõduhorisondi tüsedus, mulla pH, mullaniiskus, mulla kaaliumi- ja kaltsiumisisaldus ning luite valgustingimused.

Töö tulemustest selgub, et keskkonnatingimused, mis määravad metsastunud luidetel alustaimestiku liigirikkuse ja koosluse struktuuri, moodustavad omavahel seotud keerulise süsteemi, mis mõjutab alustaimestiku moodustanud eluvorme erinevalt.

Läbi ajaloo on luitemetsad pakkunud inimestele loendamatul hulgal erinevaid ökosüsteemi teenuseid – korilusest ökoteraapia ja rekreatsioonini. Everard jt (2010) on oma uurimistöös leidnud, et luidete ühiskondlikku väärtust on alahinnatud ning kaitse-eesmärgid ei ole võrreldavad luidete kui ökosüsteemi poolt ühiskonnale pakutavate teenuste hulgaga, lisaks on suurem osa kaitsemeetmetest suunatud ainult bioloogilise mitmekesisuse kaitsele.

Inimtegevus on läbi aegade luiteid muutnud – nende kuju ja alustaimestiku liigilist koosseisu. Seejuures mõjutavad luitemetsade alustaimestikku enim matkajad, mootorsõidukid ja erinevad rekreatiivsed tegevused (Brunbjerg jt 2015, Grunewald 2006). Käesolevas töös uuritud alad kuuluvad erinevate kaitsealade piiresse, kus on kohaldatud erinevaid kaitsekorralduslikke võtteid. Jalgsi matkavatele inimestele ei ole uuritud alal piiranguid seatud ning tulemuseks on ohtralt jalgradu, kus alustaimestik ja mullakamar on rikutud või hävinud. Kutiel jt (1999) on oma uuringutes leidnud, et hulga vähese kasutusega jalgradade tekitatud kahju on suurem võrreldes üksikute, aga ohtra kasutuskoormusega jalgradadega. Kaitseala haldajate hinnangul on eriti hävitavalt mõjunud suure maastikuläbivusega sõidukite kasutamine luitealadel (LPMP 2017) ning selle mõju kahandamiseks tuleks suurendada inimeste teadlikkust ja järelevalvet kriitilistes piirkondades.

Metsamajanduses mõjutab puistu uuenemist luitemetsades suurel määral alustaimestik. Puistu uuenemise seisukohalt peab teadma, et osa liike, nagu näiteks luitemetsades laialt levinud harilik kukemari (*Empetrum nigrum*), kanarbik (*Calluna vulgaris*), harilik palusammal (*Pleurozium schreberi*) ja harilik laanik (*Hylocomium splendens*), takistavad uuenemise seisukohast puuseemnete idanemist ja seemikute arenemist (Örd 1972a, Steijlen jt 1995, Nilsson jt 2000). Kaitsealadel on raied reguleeritud looduskaitseseaduse (2004), kaitsealade kaitse-eeskirjade (LNRPR 2006, ULPFPR 2016) ning kaitsekorralduskavadega (UPMP 2016, LPMP 2017). Raiete eesmärk ei ole majanduslik kasu, vaid looduskaitseliste eesmärkide täitmine. Luidetel asuvaid männimetsi on sajandi vältel majandatud turberaiete ja valikraie abil (Örd 2000). Praegu kehtiv metsaseadus (2006) annab võimaluse kasutada kaitsealadel kaitse-eesmärgi saavutamiseks kujundusraiet. Kui eesmärgiks on tagada piisav metsauuendus, siis tuleb kõrgemate luidete harjadel ja jalamitel eelistada turberaietest aegjärkset raiet, vältides alustaimestiku rikkumist või hävimist luidete järsematel nõlvadel. Piirkondades, kus alustaimestikus domineerivad kukemari ja/või tiheda vaibana palusammal ning laanik, tuleb vajaduse korral läbi viia maapinna osaline mineraliseerimine (Örd 1972, Kõresaar 2003). Kui raiete eesmärk on tekitada liivaseid alasid, mis on vajalikud osa liikide elutegevuseks ja paljunemiseks (näiteks kivisisalik), tuleb kõrgemate luidete lõuna- ja läänepoolsetel nõlvadel eelistada häilraiet. Tulemuseks on päikese ja tuule mõjule avatud alad, mille tagajärjel tekivad taimestikuvabad või samblikurikkad alad (Örd 1972).

Vajadus edasiseks uurimiseks

Antud alasid tuleks teatud ajavahemiku tagant seirata, sest luitemetsad on oma toitainetevaese ja happelise mulla tõttu madala puhverdusvõimega ökosüsteemid. Suurenenud on nende vähese koormustaluvusega alade rekreatiivne koormus ja atmosfääri lämmastiku depositsioon, mis võib negatiivselt mõjutada luitemetsade tundlikku ökosüsteemi ning sealset liigirikkust.

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I

ORIGINAL PUBLICATIONS

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SPECIAL FEATURE: ORIGINAL ARTICLE

Approaches for forest disturbances studies: natural variability and tree regeneration

Ground vegetation under natural stress conditions in Scots pine forests on fixed sand dunes in southwest Estonia

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Abstract Ecosystems on dunes are influenced by critical environmental factors (mineral nutrients, water deficiency, etc.) considered decisive for their existence. The present paper is based on studies carried out on dunes on the coastal area of the Baltic Sea, southwest Estonia. The nature of forest ecosystems on dunes was studied from the aspects of chemical characteristics of soil, vascular plant species richness and diversity. Sampling sites on the dunes with different heights were selected in *Cladina* and in *Vaccinium vitis-idaea* site-type Scots pine forests. Vascular plant species richness and diversity were related to edaphic gradients. On the dune with a height of 32.1 m a.s.l., significant relationships were revealed between the number of species of ground vegetation, pH, volumetric water content in soil and the position of the sample plots. No relationships were revealed between the number of vascular plant species, soil pH, volumetric water content and mineral nutrients on the dune with a height of 9 m a.s.l. The most frequent and abundant plant species on the higher dune were *Deschampsia flexuosa*, *Vaccinium vitis-idaea* and *V. myrtillus*; the highest number of species were found at the bottom of the dune, while on the top only some xeromorphic species such as *Festuca ovina*, *Sedum acre* and *Crepis tectorum* occurred. On the lower dune, the most frequent were *Vaccinium vitis-idaea, V. myrtillus* and *Melampyrum pratense*, while *V. uliginosum* was found only on the bottom and slope and *Empetrum nigrum* on the top of the dune.

Keywords Coastal dunes · Ground vegetation · Scots pine forest · Soil chemistry

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Introduction

Plants in nature may be exposed, during their ontogeny, to a wide variety of favourable or disadvantageous biotic and abiotic factors. Water and nutrient deficits affect every aspect of plant growth, being serious environmental factors determining patterns and variety of plant communities and vegetation in general (van der Maarel 1997; Koehler 1998; Isermann 2005). The vegetation on the dune landscape is influenced by very different edaphic and climatic factors, as a rule by water and nutrient deficiency and relatively high wind speeds on the top compared with the situation at the bottoms of dunes. Estonian, Latvian and Lithuanian western seacoasts are rich in sand dunes of different ages and there are Scots pine (*Pinus sylvestris* L.) forests on already stabilised dunes. The dunes in southwest Estonia, of up to 20–25 m relative height (32–35 m a.s.l.), were formed during the transgressive phases of the Baltic Ice Lake, the Ancylus Lake and the Litorina Sea (Eltermann and Raukas 1966; Martin 1978; Raukas 1997; Ratas and

Rivis 2003). Formation of higher dunes was hindered by the small supply of sand, humid climate and continuing slow land uplift (Orviku et al. 2003). In most countries of the Baltic Sea Region, the pressure on the environment in the coastal areas has been increasing considerably. Since the end of the twentieth century, tourism has been the most destructive human activity affecting coastal areas (van der Meulen 1997; Jarmalavičius 2005), and it has had a negative influence on the vegetation cover and relief of dunes (Olšauskas 1996; Olšauskas and Olšauskaitė-Urbonienė 2001; Łabuz 2004). Today, fixed dunes are important for biodiversity at species and plant community levels, and they are considered as a priority habitat by the European habitat directive (Council of the European Communities 1992). Numerous scientists have studied forests on dunes in southwest Estonia; however, studies on the relationships of the soils and vegetation cover characteristics in dune systems are still lacking.

The purposes of this study were to conduct a basic research on the vascular plant species composition and on some characteristics of soil on dunes related to the height and the position of the sample plots. Attention was focused on soils and plant communities in *Pinus sylvestris* L. forests of *Cladina* and *Vaccinium vitis-idaea* site types on typical sand dunes in Estonia on the coast of the Gulf of Riga in the eastern part of the Baltic Sea.

Materials and methods

Field studies were carried out in 2006 and 2008 on two typical dunes in southwest Estonia in the coastal area of the Baltic Sea. By today, the dunes have become fixed and covered with single-species Scots pine stands of natural origin and varying age of 120–190 years. Stands with densities in range 0.4–0.45 belong to III quality class. Predominant soils on the dunes are acidic Podzols (Mandre 2003; Ratas and Rivis 2003).

For the investigation of ecosystems on dunes, following sites were selected:

- Site No. 1 (Tõotusemägi) is located 58°7′56″N, 24°30′36″E and reaches 32.1 m a.s.l. Dune belong to Cladina forest site type on the top and the *Vaccinium vitis-idaea* site type on the slopes. Sample plots for the determination of soil characteristics on the dune were located on the bottom, on the slope and on the top, respectively 12, 20 and 32 m a.s.l.
- Site No. 2, located 58°13′51″N, 24°30′47″E, belongs to the *Cladina* forest site. It was the lowest site in the present study with an absolute altitude of 9 m. The sample plots for the determination of soil horizons on the dune were located at heights of 3, 5 and 9 m a.s.l (Mandre et al. 2006, 2008).

Below, site No. 1 is referred as higher dune and site No. 2 as lower dune.

Climatically, the influence of the Baltic Sea is strongly felt in the area. According to the closest weather station of the Estonian Meteorological and Hydrological Institute in Pärnu, the main climate characteristics during the period of our investigations in 2006–2007 were as follows: average annual temperature 7.4°C with maximum average of 18°C in August and minimum average of −9.4°C in February; total precipitation 767 mm. Relative air humidity was 80% in the area.

Descriptions of the plant communities were made in quadrats of 1 × 1 m at different heights on the dune, sample plots were located on the western plain in front of the dune and on its bottom, slope and top forming a continuous transect, 19 quadrats were analysed on the higher dune and 17 on the lower dune. In the quadrats, the species composition and coverage of vascular plants were determined following Kalda (1970), Masing (1979) and Manual for Integrated Monitoring (1993). Coverage of bryophytes and lichens were assessed, but although mosses and lichens represent an important part in species richness and biodiversity, they were left out of analyses in the current study because they do not possess roots and are not expected to show direct relationships with nutrients in the soil (Kooijman et al. 1998).

Soil horizons were distinguished to the depth of 1 m from the surface and their thickness was measured. Soil subsamples ($n = 3$) were collected from the bottoms, slopes and tops of the dunes. Combined samples from mineral topsoil (up to the depth of 30 cm) were analysed for the determination of their chemical peculiarities (N, P, K, Ca and Mg) and pH. Volumetric water content (VWC, %) in soil was determined for three periods with Field Scout^{TM} TDR 300 at a depth of 20 cm ($n = 3$). The collected soil samples were air-dried (40°C) and sieved through a 2-mm sifter. Soil pH was measured ($n = 5$) in a soil–water suspension (ISO/10390 1994) using a laboratory pH-meter (Mettler Toledo MP220). The concentrations of N, P, K, Ca and Mg available to plants were determined in the Plant Biochemistry Laboratory of the Estonian University of Life Sciences, P and K were determined by the Egner–Riehm double lactate method, and Ca and Mg by the Egner–Riehm–Domingo ammonium acetate–lactate method (ISO/11260 1995). Total N was determined by the Kjeldahl method (ISO/11261 1995).

The data obtained were processed statistically to find relationships between the height of the dune and the concentrations of nutrients in soil and abundance of species on sample plots. Regression analyses were carried out and coefficients (R^2) were calculated using Statgraphics and MS Excel 2003. Significance of differences was accepted at $p < 0.05$.

Results

On the dune landscape, a thin A-horizon existed only on the bottoms of the dunes. The thickness of the A-horizon varied in the range 2–20 cm (with an average of 8 cm). The thickness of O-horizons was variable, being 4–30 cm (with an average of 12.5 cm) on the bottoms and significantly thinner on the slopes and on the tops of the dunes (5–10 cm).

Analysis of the soils on dunes indicated that the upper layers of soils were predominantly acidic (pH_{H2O} 3.8–6.1) and poor in mineral nutrients and water (Table 1). Relationships were found between the VWC, concentration of Ca and the location of the sample plot on the dune (subsequently $R^2_{VWC} = 0.912$, $p = 0.0001$ and $R^2_{Ca} = 0.646$, $p = 0.0058$).

Descriptions of the plant communities revealed noticeable differences in the number of species between the sample plots on the bottoms, slopes and tops of the higher dune, but on the lower dune differences were not so noticeable (Fig. 1). Altogether, 23 different vascular plant species were mentioned (Table 2). The number of vascular plant species was related to the position of the sample plots on the higher dune ($R^2 = 0.738$). On the lower dune, no relationship between the number of species and the location of the sample plot was detected. The number of species on the higher dune, but not on the lower dune, was related to the pH, VWC of the soil ($R^2_{pH} = 0.977$; $R^2_{VWC} = 0.988$) and concentrations of N%, K, Ca and Mg ($R^2_{N\%} = 0.999$, $R^2_K = 0.962$, $R^2_{Ca} = 0.780$, $R^2_{Mg} = 0.794$). The species number of vascular plants in the ground cover on the plain before the higher dune (site No. 1) and at its bottom was 4 times as high as on its top. On this dune, the most frequent and abundant was *Deschampsia flexuosa*, which was represented in 89% of the quadrats. Other frequently occurring species were *Vaccinium vitis-idaea* in 68%, *Melampyrum pratense* in 52% and *V. myrtillus* in 47% of the quadrats. Regarding the number of species, the sample plots on the transect differed markedly. On the sample plots located on the bottom of site No. 1, *V. myrtillus*, *Oxalis acetosella* and *D. flexuosa* were most abundant. Only some xeromorphic species such as *Festuca ovina*, *Sedum acre* and *Crepis tectorum* occurred on the sample plots on the top of the dune. Site No. 2 had much poorer vegetation. The most frequent plant species there were *V. vitis-idaea, V. myrtillus* and *M. pratense* (Table 2) occurring in all quadrats, while *V. uliginosum* was found only on the bottom and slope of the dune and *Empetrum nigrum* mostly on its top. The coverage of vascular plant species, bryophytes and lichens varied on the higher dune, while changes in the coverage values on lower dune were not noticeable (Fig. 1).

Discussion

As found in the present study, soils on the dunes are acidic Podzols (pH 3.8–6.1), which are generally poor in humus, water and mineral nutrients. The pH values of the soil of the higher dune showed a statistically significant relationship with the number of species on the sample plots, the soil pH being lower on the sample plots where the number of species was higher. Isermann (2005) found that variability in soil pH tended to increase with increasing species diversity. This is in accordance with the standpoint of Marschner (1995) about the dependence of the pH in the rhizosphere surrounding the root surface of plants, because the plants are able to decrease the pH in soil. A few species with high abundance might have the same effect. On the lower dune, this relationship was not revealed, the number of vascular plant species not differing significantly between the sample plots.

The soil water availability influences the establishment and distribution of vegetation across the dune (Baldwin and Maun 1983). Measurements of VWC in soil on the higher dune showed a rapid decrease toward its top, which can be

Table 1 Total concentration of mineral elements, water content and pH of mineral topsoil at a depth of 30 cm from the surface

Sampling site	Position and height (m a.s.l.) of sample plots on dune	VWC (%)	pH_{H2O} ($n = 5$)	N		P		K		Ca		Mg	
				%	%[a]	mg kg^{-1}	%[a]	mg kg^{-1}	%[a]	mg kg^{-1}	%[a]	mg kg^{-1}	%[a]
Site no. 1	Bottom (12 m)	13.1	3.8	1.93	100	63.7	100	666	100	460	100	286	100
	Slope (20 m)	3.9	5.5	0.44	77	28.1	56	280	58	302	33	206	28
	Top (32 m)	1.2	6.1	0.20	89	77	22	114	83	103	78	111	61
Site no. 2	Bottom (3 m)	13.0	4.3	0.34	100	21.8	100	113	100	310.5	100	77.4	100
	Slope (5 m)	4.5	4.4	0.33	3	33.5	54	132.2	17	299.3	4	83.0	7
	Top (9 m)	1.7	4.3	0.26	24	32.1	47	122.9	9	255.3	18	78.6	2

VWC volumetric water content in soil at a depth of 20 cm

[a] Difference from the concentration on the bottom (100%)

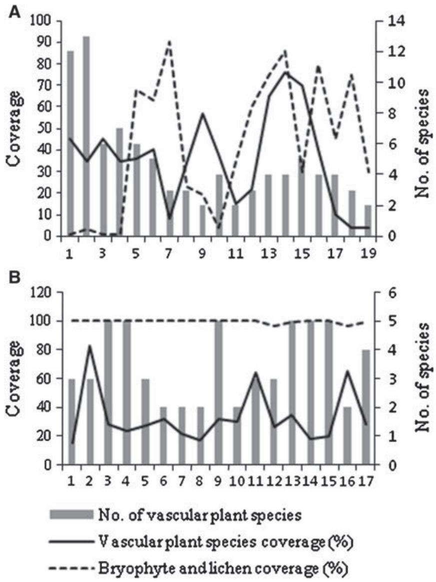

Fig. 1 Number of vascular plant species, coverage of ground vegetation and coverage of bryophytes and lichens along the transect on **a** site No. 1 and **b** site No. 2

Table 2 The list of vascular plant species and their frequency on sites No. 1 and No. 2

Species	Site No. 1	Site No. 2
Deschampsia flexuosa	17	0
Vaccinium vitis-idaea	13	17
Melampyrum pratense	10	13
Vaccinium myrtillus	9	12
Calluna vulgaris	6	7
Sorbus aucuparia (seedlings)	5	0
Oxalis acetosella	4	0
Convallaria majalis	4	0
Calamagrostis arundinacea	4	0
Frangula alnus	3	0
Trientalis europaea	3	0
Festuca ovina	3	0
Solidago virgaurea	2	0
Rubus saxatilis	2	0
Crepis tectorum	2	0
Picea abies (seedlings)	1	0
Dryopteris carthusiana	1	0
Lysimachia vulgaris	1	0
Calamagrostis epigeios	1	0
Sedum acre	1	0
Empetrum nigrum	0	4
Vaccinium uliginosum	0	3
Festuca rubra	0	3

related to the variation of the vegetation cover. Firstly, on the bottom of the dune, the horizontal cover value is higher and the number of species is higher, lowering the surface temperature and lessening evaporation. Secondly, the thicker O- and A-horizons on the bottom create a greater water-holding capacity. On the lower dune, the number of species was not related to the VWC, the main reason may be that the vegetation cover is not so varied.

Dune landscape heterogeneity creates micro-habitats with quite different growth conditions (concentrations of macro-nutrients, pH, VWC); such spatial variation provides a broad range of habitats where distinct niches could co-exist (Sack and Grubb 2002). On the observed dunes, the Scots pine stands with floristically poor undergrowth were prevalent. In all, 21 plant species were observed on the typical higher sand dune (site No. 1) in the studied area. The most frequent species there was *D. flexuosa*. Other frequently occurring species were *V. vitis-idaea*, *M. pratense* and *V. myrtillus*. The number of species on the transect on the dune differed markedly from the bottom to the top. The highest number of species was found on the bottom of the dune, which can be explained by the favourable soil conditions. The nutritional and water conditions in the upper zones of the dunes are less favourable for species distribution, and on the tops of the dunes only dispersed xeromorphic species like *F. ovina*, *S. acre* and *C. tectorum* occurred. The number of species on site No. 1 was statistically related to the position of the sample plots on the dune, the soil pH, VWC and concentrations of the macro-nutrients (except for P). The results are consistent with the often proposed positive correlation between environmental variability and species richness (Jackson and Caldwell 1993). On the lower dune (site No. 2), the ground vegetation was floristically much poorer when compared to the transect on the relatively higher dune (site No. 1). In all, seven plant species were observed there, the most frequent being *V. vitis-idaea*, *V. myrtillus* and *M. pratense*, while *V. uliginosum* was found only on the bottom and slope of the dune and *E. nigrum* on its top. The number of vascular plant species was not affected by the location of the sample plots, perhaps because the growth conditions do not change so rapidly. The species distribution on the lower dune (site No. 2) did not show any relationships with the soil pH, concentrations of the macro-nutrients and VWC.

To conclude, it should be said that the patterns of species richness in coastal areas are not homogeneous but vary across the vegetation mosaic and are related to the height of the dune. On relatively higher dunes, the micro-environmental variation of soils, and the variability of soil chemical composition, pH and VWC, have important implications for vascular plant species distribution. On the relatively lower dune, no relationships were detected between the number of vascular plant species and the investigated growth conditions.

Nowadays, coastal dunes are popular areas for recreation, but they are fragile ecosystems that can be easily destroyed through trampling and other human activities. In general, it is necessary to maintain existing forests and other coastal biotopes, acknowledging the international importance of biological diversity in coastal areas.

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II

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Effects of environmental factors on the species richness, composition and community horizontal structure of vascular plants in Scots pine forests on fixed sand dunes

Tilk M., Tullus T., Ots K. (2017). Effects of environmental factors on the species richness, composition and community horizontal structure of vascular plants in Scots pine forests on fixed sand dunes. Silva Fennica vol. 51 no. 3 article id 6986. 18 p. https://doi.org/10.14214/sf.6986

Highlights

- Factors affecting the species richness, composition and horizontal structure of vascular plants are related to dune topography, resulting in the differentiation of soils and therefore complexes of different microhabitats that are populated by various vascular plant species and causing vegetation zonation.

Abstract

Different environmental factors were studied to determine which factors influence the species richness, composition and structure of vascular plants in *Pinus sylvestris* L. forests in a fixed dune landscape in south-western Estonia. In addition to site topographic factors, different environmental parameters were investigated. Thirty-four vascular plant species were recorded in 232 quadrats. The most abundant species was *Vaccinium vitis-idaea* L., which was in 82.8% of quadrats, followed by *Vaccinium myrtillus* L. (74.1%), *Melampyrum pratense* L. (71.1%) and *Deschampsia flexuosa* (L.) Trin. (69.8%). The multiple response permutation procedure (MRPP) showed considerable differences in species composition at the bottoms of dunes compared with that on the slopes and at the tops of dunes. Indicator species analysis (ISA) determined species exhibited characteristics specific to zone: *V. myrtillus* had the highest indicator value at the bottoms of dunes; *Calluna vulgaris* L., at the tops. Soils were Haplic Podzols, and the presence of humus horizon depended on zone. Soil conditions on the dunes were variable and site specific, in general, soils at the bottoms of the dunes were more acidic and moist compared with those of the slopes and tops of the dunes, and the nutrient content decreased toward the dune tops. According to non-metric multidimensional scaling (NMDS) and linear mixed model analyses, species coverage, composition and richness were controlled by site-specific factors such as absolute height, location and aspect of the quadrat on the dune; soil nitrogen, potassium and phosphorus contents; soil pH and moisture; light conditions; and the thickness of the litter horizon.

Keywords biodiversity; inland dunes; microhabitats; soil conditions; vegetation–site relationships
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1 Introduction

The wooded dunes of the boreal region are among the priority habitats according to the Council of European Union (1992). In Europe, wooded dunes are primarily sea dunes of the Atlantic Ocean, Mediterranean Sea, North Sea and Baltic Sea coasts. Fixed dune landscapes are usually characterised by specific topographical features that vary in aspect, slope angle and microclimate. Plant communities differ on slopes facing different cardinal directions; some species are generally confined to specific zones (Houston 2008; Mandre et al. 2008; Tilk et al. 2011). There have been numerous studies concerning coastal dunes and their vegetation, growth conditions and vegetation changes induced by disturbances (Kutiel et al. 1999; Kooijman and Besse 2002; Ensign et al. 2006; Isermann 2008; Brunbjerg et al. 2015; Ciccarelli 2015; Pinna et al. 2015). Topography, human influence, and soil conditions such as pH, nutrients and moisture are important factors that affect ground vegetation in dune areas (Isermann 2005; Ruocco et al. 2014; Sewerniak et al. 2017). In Estonia, Ilves (1966), Eltermann and Raukas (1966), Raukas (1968), Örd (1972, 1973) and Mandre et al. (2008) studied the aspects of fixed dune history and soils in the Rannametsa dune area. Vascular plant diversity in the same dune area has been studied by Mandre et al. (2006) and Tilk et al. (2011). However, these studies included data from one or two dunes and focussed on one slope of the dunes, but it is known that dune vegetation, soil conditions and even forest site type can differ drastically between slopes (Raukas 1968; Örd 1972). Research on dune habitats is vital. The current assessments of dune habitats indicate an unfavourable conservation status (European Commission 2015), and to acknowledge the temporal changes (like climate warming, atmospheric nitrogen deposition) and increasing recreational pressure on these areas, further actions should be implemented. However, valuable complex and statistically relevant information about fine-scale variations in ground vegetation communities and their relationships to soil resources and growth conditions on *Pinus sylvestris* L. forested inland dunes is still lacking. The objective of this paper is to provide new knowledge concerning ground vegetation in dune forests and to determine which environmental (light and soil conditions) and topographical factors affect the vascular plant species richness and composition of the ground vegetation and are therefore responsible for ground vegetation zonation. As such, the following hypothesis was formed:

- Dune forest ground vegetation forms different vegetation zones and patches along the dune profile primarily on higher dunes where growth conditions such as soil moisture and nutrient contents change more rapidly than on significantly lower dunes; therefore the absolute and relative heights of the dune are important topographical features that cause the zonation of vascular plant species.

2 Material and methods

2.1 Description of the study area

The studied dune system is situated in south-western Estonia. To investigate the ecosystems on dunes of different heights, four sampling sites were selected (Fig. 1). Dunes in the studied area were formed by Lake Ancylus and the Littorina Sea during the ice ages and are with different heights: site 1 absolute height 28 m and relative height 16 m; site 2 absolute height 33 m and relative height 21 m; site 3 absolute height 12 m and relative height 6 m; site 4 absolute height 10 m and relative height 6 m.

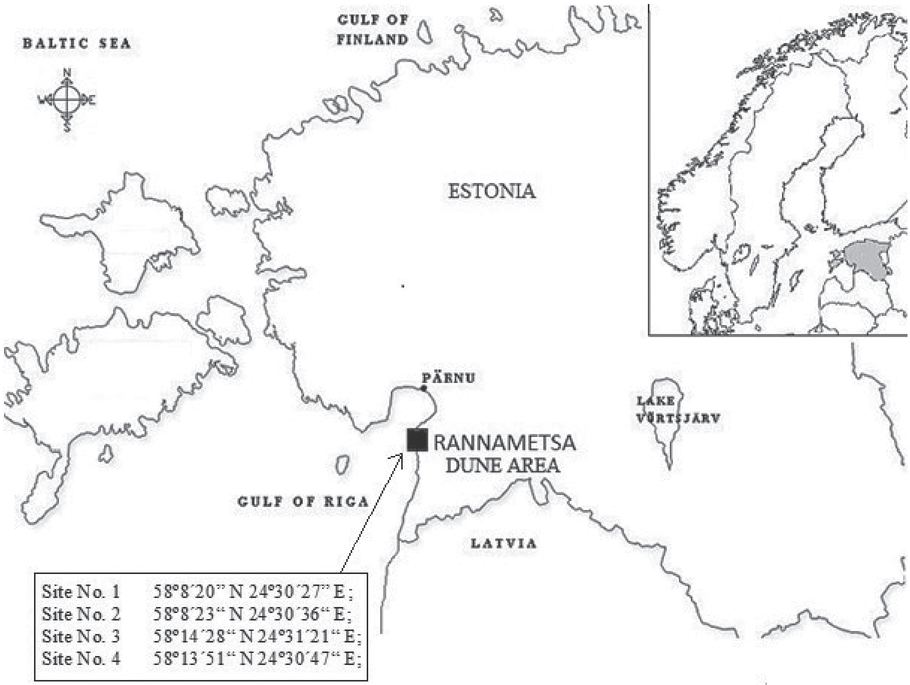


Fig. 1. Location of study area and study sites.

Lower dunes are situated in the Uulu-Võiste landscape protection area, where three priority habitats according to the European Commission (2013) are present: wooded dunes of the Atlantic, Continental and Boreal region (type 2180); Western Taïga (type 9010*); and Fennoscandian deciduous swamp woods (type 9080*). Higher dunes are located in the Luitemaa nature reserve, where fixed coastal dunes with herbaceous vegetation (grey dunes) (type 2130*); wooded dunes of the Atlantic, Continental and Boreal region (type 2180); and humid dune slacks (2190) are under protection.

2.2 Climate

According to the closest weather station of the Estonian Meteorological and Hydrological Institute in Pärnu, the main climate characteristics during the period of investigation in 2008 were as follows: average annual temperature of 7.6 °C, with a maximum average of 16.6 °C in July and a minimum average of –0.6 °C in January; total precipitation of 862 mm, with a maximum of 147.5 mm in August and a minimum of 17 mm in May. The relative humidity was 83%. The length of the thermal growing period (temperature greater than 5 °C) was 232 days (30.03.2008–17.11.2008). During the winter of 2007/2008, no permanent snow cover was recorded, but throughout the winter, there were 48 days with snow.

2.3 Methods

Field studies to analyse ground vegetation were carried out in 2008. Sample plots that formed continuous transects over the dunes were established on all four dunes. Transects started from the plain in front of the dune and extended over the top to the back plain in increments of 1 m. The descriptions of the plant communities were made in quadrats 1 × 1 m in size at different heights on the dunes; altogether, 232 quadrats were studied.

The transect at site 1 started from the southern plain of the dune and extended continuously over the top of the dune to the northern plain; altogether, 58 quadrats were analysed. The transect at site 2 extended from the western plain over the top to the eastern plain and encompassed 108 quadrats. At site 3, the sample plots (n=32) extended from the southern plain to the northern plain, and at site 4, the transect of sample plots (n=34) was directed from east to west.

Average characteristics for the studied stands were obtained from the State Forest Management Centre database and are presented in Table 1. Forest site type is in accordance with those of Lõhmus (2004).

The species composition of vascular plants in the quadrats was determined in May, July and September to record seasonal features of the vegetation and therefore the complete species composition (Kalda 1966; Masing 1979). The nomenclature follows the keybook of Estonian vascular plants (Leht 2010). Dominant species were determined based on abundance (Braun–Blanquet five-point cover scale). The total cover of the vascular plant layer, the total cover of the bryophyte and lichen layers and the cover of each vascular plant species in the quadrats were estimated visually using a scale of 1–100%.

Canopy cover as a measure of the percentage of forest floor covered by the vertical projection of tree canopies was estimated in every quadrat. To evaluate the amount of light transmitted through the canopy to the ground vegetation, below-canopy photosynthetically active radiation (PAR, $\mu mol\ m^{-2}\ s^{-1}$) was measured (n = 10 per quadrat) with Decagon Devices AccuPAR (Model PAR-80) light-interception device at midday on 23.07.2008 (sunny, clear conditions). Because light is highly variable, measurements were performed during a short period (from 11.00 to 13.00) at all sites. Quadrats angles were measured to describe micro-topographical features using an inclinometer for every quadrat and values were classified according angle degree to five classes: 1 (1–10°); 2 (11–20°); 3 (21–30°); 4 (31–40°); and 5 (41–50°). Absolute altitudes were measured using a Garmin GPSMap 76CSx device and relative height was calculated using first quadrat of the transect as a zero.

Table 1. Average characteristics of the investigated stands.

Site No.	Soil type	Forest site type	Composition of trees	No. of trees per hectare	Age, yr	Site quality index	Canopy cover	Height, m	Breast height diameter, cm	Density of understory
1	Haplic Podzol	*Rhodococcum*	100 Ps	149	180	IV	0.45	24	37	Low
2	Haplic Podzol	*Cladonia*	100 Ps	191	190	IV	0.54	24	36	Low
3	Haplic Podzol	*Cladonia*	100 Ps	98	200	IV	0.62	21	44	Low
4	Haplic Podzol	*Cladonia*	100 Ps	143	210	IV	0.60	23	38	Low

Ps = *Pinus sylvestris*

Soil volumetric water content (VWC, %) was determined in every quadrat using a Field Scout^{TM} TDR 300 at a depth of 20 cm (n = 3 per quadrat) to describe soil water-holding capacity. Soil VWC data were collected in May, July and September when no rain had occurred for at least 3 days before measurements.

All soil types were classified according to the FAO (FAO-ISRIC-ISSS 1998). Soil samples from every quadrat were collected in July 2010 at a maximum depth of 20 cm to measure pH and electrical conductivity. The soil pH and electrical conductivity (EC; µS) were measured in soil: water mixtures (1:2.5 or 1:5) using a Eutech Instruments PC300 pH/conductivity meter. To analyse the nitrogen, phosphorus, potassium, calcium and magnesium contents, soil samples were collected; soil horizons were distinguished by bottoms, slopes and the tops of dunes (n = 3 at every location, 15 samples per dune) collected at a maximum depth of 20 cm, as most roots for majority of vascular plants are concentrated in the first 20 cm (Bednarek et al. 2005; Solon et al. 2007). The contents of total nitrogen, phosphorus, potassium, calcium and magnesium in the top soil samples were determined at the Laboratory of Plant Biochemistry of the Estonian University of Life Sciences. The soil samples were analysed for their extractable content of phosphorus (ammonium lactate; FIAStar 5000 (flow injection analyser)), potassium (ammonium lactate; flame photometric method), calcium (ammonium acetate; flame photometric method), magnesium (ammonium acetate; FIAStar 5000 (flow injection analyser)) and total nitrogen (copper catalyst; Kjeldahl method).

2.4 Data analysis

The species richness of vascular plants was estimated for every quadrat as the number of species present in the quadrat. Microsoft Excel 2010 was used to perform basic statistical analysis.

One-way ANOVA followed by post-hoc Tukey HSD test using Tukey-Kramer method was applied to determine significant differences between environmental characteristics at different locations on dunes (Vasavada 2016). Level of significance of $a = 0.05$ was used. For the statistical analysis, transects on dunes were divided into three zones/locations: plain before the dune, slope and top, based on the relative height and the angle of the quadrat.

The effect of grouping factors on species composition was tested using the multiple response permutation procedure (MRPP) (Mielke et al. 1976). To correct the p-values for multiple comparisons using MRPP, a Bonferroni correction was applied. Indicator species analysis (ISA) (Dufrene and Legendre 1997) was conducted to specify indicator species for different zones. The statistical significance of indicator values was proven using the Monte Carlo simulation technique. MRPP and ISA were performed using PC-ORD Version 6 (McCune and Mefford 2011). Overlapping and individuality of species at different sites and zones on dunes were described using a Venn diagram, made using Venny (Oliveros 2015).

To study variation in vascular plant species composition and to determine its influencing factors, non-metric multidimensional scaling (NMDS) ordination was performed using the free statistical software R Version 3.2.3, with the community ecology package "Vegan". A linear mixed model (with dune as a random factor) was applied to clarify the effects of environmental variables (light conditions, soil moisture, soil pH, macronutrient contents, litter horizon thickness, and the cover of the bryophyte and lichen layers) and location (zone, aspect and absolute height of the quadrat) on species richness and the total cover of vascular plants. Due to intercorrelation between canopy cover and PAR, canopy cover was left out of model. Q-Q plots and residual distributions were used to assess the normality of model residuals.

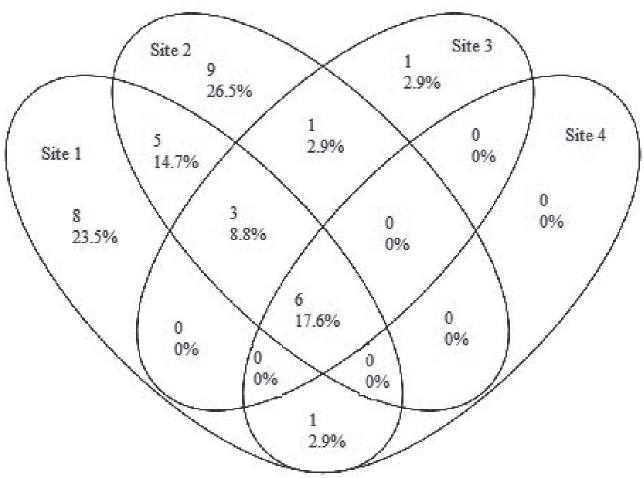
3 Results

3.1 Species composition

Thirty-four species of vascular plants belonging to 18 families were recorded in transects. The most represented family was the Poaceae with four species, followed by the Asteraceae (three species), Ericaceae (three species), Juncaceae (three species), Liliaceae (three species) and Vaccinaceae (three species).

There were six vascular plant species present at all sites: *Calluna vulgaris* L., *Vaccinium myrtillus* L., *Melampyrum pratense* L., *Empetrum nigrum* L., *Festuca polesica* Zapal. and *Vaccinium vitis-idaea* L.. Overlapping and individual species on different dunes are shown in Fig. 2.

At site 1, 23 species occurred with *Deschampsia flexuosa* (L.) Trin. in 100%, *V. myrtillus* in 89.7% and *V. vitis-idaea* in 86.2% of the quadrats. The highest number of species was recorded at site 2, where 24 vascular plant species were found; the most frequent vascular plant species



Sites	No.	Species
Sites 1, 2, 3 and 4	6	*Calluna vulgaris*; *Vaccinium myrtillus*; *Melampyrum pratense*; *Empetrum nigrum*; *Festuca polesica*; *Vaccinium vitis-idaea*;
Sites 1, 2 and 3	3	*Deschampsia flexuosa*; *Luzula pilosa*; *Trientalis europaea*;
Sites 1 and 2	5	*Polygonatum odoratum*; *Arctostaphylos uva-ursi*; *Convallaria majalis*; *Lycopodium annotinum*; *Epilobium angustifolium*;
Sites 1 and 4	1	*Vaccinium uliginosum*;
Sites 2 and 3	1	*Festuca rubra*;
Site 1	8	*Stellaria graminea*; *Aegopodium podagraria*; *Rubus idaeus*; *Carex digitata*; *Maianthemum bifolium*; *Deschampsia caespitosa*; *Oxalis acetosella*; *Mycelis muralis*;
Site 2	9	*Hieracium umbellatum*; *Carex caryophyllea*; *Monotropa hypopitys*; *Campanula patula*; *Luzula multiflora*; *Lycopodium clavatum*; *Silene dioica*; *Solidago virgaurea*; *Luzula campestris*;
Site 3	1	*Ledum palustre*;

Fig. 2. Venn diagram showing the overlapping and individuality of vascular plant species at different sites.

Table 2. The results of multiple response permutation procedure (MRPP) tests for the comparison of species composition on different dunes.

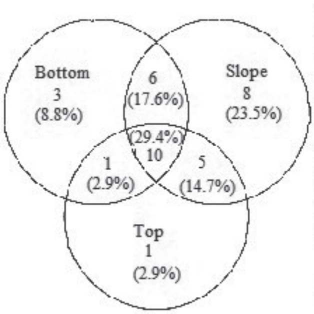
Test pair	Site 1 vs. Site 2	Site 1 vs. Site 3	Site 1 vs. Site 4	Site 2 vs. Site 3	Site 2 vs. Site 4	Site 3 vs. Site 4
p-value	**<0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**	0.011

Bold values are significant after the Bonferroni correction

recorded were *D. flexuosa* (85.2%), *V. vitis-idaea* (76.9%) and *V. myrtillus* (74.1%). At sites 3 and 4, 11 and 7 species of vascular plants were distinguished, respectively. *Melampyrum pratense* L. (84.4%), *V. vitis-idaea* (78.1%) and *F. polesica* (56.3%) were dominant at site 3, and *V. vitis-idaea* (100%), *M. pratense* (85.3%) and *V. myrtillus* (70.6%) were most prevalent at site 4. Vascular plant species were not found in the four quadrats on the upper part of the slope at site 2.

According to the results of the MRPP tests, almost all dunes differed statistically from each other, with the exception of the lower dunes 3 and 4, which did not significantly differ in vascular plant species composition (Table 2). As the MRPP results indicated considerable differences in species composition between dunes, subsequent tests to compare the effect of location on species composition were performed separately for each dune. The MRPP analyses revealed that species composition at the bottoms of all dunes differed significantly from species composition in the other zones (slope and top). However, a significant difference between slope and top was observed only on the highest dune (site 2). Overlapping species and species distribution between different zones are shown in Fig. 3.

ISA was also conducted separately for each dune, and the results showed characteristic species were causing zonation of the bottoms, slopes and tops (Table 3). Although indicator species for the bottoms and slopes were different for each dune, *C. vulgaris* was as an indicator species for tops on three dunes; *Festuca rubra* L., for two.



Location	No.	Species
Bottoms, Slopes and Tops	10	*Calluna vulgaris*; *Deschampsia flexuosa*; *Vaccinium myrtillus*; *Melampyrum pratense*; *Empetrum nigrum*; *Festuca polesica*; *Lycopodium annotinum*; *Luzula pilosa*; *Trientalis europaea*; *Vaccinium vitis-idaea*;
Bottoms and Slopes	6	*Ledum palustre*; *Maianthemum bifolium*; *Convallaria majalis*; *Vaccinium uliginosum*; *Oxalis acetosella*; *Luzula campestris*;
Bottoms and Tops	1	*Arctostaphylos uva-ursi*;
Slopes and Tops	5	*Hieracium umbellatum*; *Campanula patula*; *Festuca rubra*; *Solidago virgaurea*; *Epilobium angustifolium*;
Bottoms	3	*Rubus idaeus*; *Carex digitata*; *Mycelis muralis*;
Slopes	8	*Stellaria graminea*; *Carex caryophyllea*; *Aegopodium podagraria*; *Polygonatum odoratum*; *Monotropa hypopitys*; *Luzula multiflora*; *Deschampsia caespitosa*; *Lycopodium clavatum*;
Tops	1	*Silene dioica*;

Fig. 3. Venn diagram showing the overlapping and individuality of vascular plant species at different locations on dunes.

Table 3. Vascular plant indicator species with indicator values (IV) for different zones (bottom, slope and top) on dunes according to the indicator species analysis (ISA).

	Bottom			Slope			Top		
		IV	p-value		IV	p-value		IV	p-value
Site 1	*Rubu ida*	28	0.011	*Empe nig*	36	0.016	*Call vul*	32	0.05
	Oxal ace	25	0.041						
	Mela pra	50	0.042						
Site 2	*Empe nig*	53	0.0002				*Hier umb*	26	0.001
	Fest pol	50	0.0004				*Call vul*	50	0.001
	Conv maj	13	0.035				*Mela pra*	52	0.002
							Soli vir	26	0.002
							Fest rub	35	0.006
							Trie eur	21	0.021
Site 3	*Vacc myr*	73	0.0002	*Trie eur*	61	0.001	*Fest rub*	41	0.05
	Vacc vit	69	0.0002						
	Ledu pal	43	0.012						
Site 4	*Vacc uli*	38	0.012	*Fest pol*	48	0.025	*Empe nig*	52	0.002
							Call vul	59	0.008

Rubu ida = *Rubus idaeus*; Oxal ace = *Oxalis acetosella*; Mela pra = *Melampyrum pratense*; Empe nig = *Empetrum nigrum*; Fest pol = *Festuca polesica*; Conv maj = *Convallaria majalis*; Vacc myr = *Vaccinium myrtillus*; Vacc vit = *Vaccinium vitis-idaea*; Ledu pal = *Ledum palustre*; Vacc uli = *Vaccinium uliginosum;* Trie eur = *Trientalis europaea*; Call vul = *Calluna vulgaris*; Hier umb = *Hieracium umbellatum*; Soli vir = *Solidago virgaurea*; Fest rub = *Festuca rubra*.

3.2 Environmental variables

Soil horizons were distinguished through 20 cm. Site 1 represented a *Rhodococcum* forest site type, with Haplic Podzol and humus horizon (1–7.5 cm) soil at the bottoms and Haplic Podzol soil on the slopes and on top of the dune.

Site 2 belonged to a *Cladonia* forest site type, with Haplic Podzol and humus horizon (1–7 cm) soil at the bottoms and on the slopes of the dune and Haplic Podzol soil at the top of the dune.

Site 3 belonged to the *Cladonia* forest site type, with Haplic Podzol soil on the southern bottom slope and at the top of the dune, Haplic Podzol and humus horizon (1–15 cm) soil on the northern slope and Carbi-Saprihistic Podzol on the northern bottom.

Site 4 belonged to the *Cladonia* forest site type, with Haplic Podzol soil on the bottoms and eastern slope and at the top of the dune. The western slope soil type was a Haplic Podzol with a humus horizon (1–2 cm). Soil and light characteristics are presented in Table 4.

Average soil moisture was 8.2% (VWC) but ranged from 0.7% to 43.9%. In general the driest quadrats were located at the tops of the dunes, whereas the moistest were at the bottoms; on the slopes, the volumetric water content was in between that of the tops and bottoms. The highest soil moisture value (43.9%) was recorded at site 3, where the northern bottom of dune a Carbi-Saprihistic Podzol was present. The lowest average soil moisture value (0.73%) was recorded on the upper part of the slope at site 2 in a quadrat where the vascular plant species cover was nearly zero. The soil volumetric water content was seasonally variable; significant differences in soil water content were recorded between spring, summer and autumn. Soil moisture was highest in autumn and was 55% higher than the vegetation period average. The driest period was spring, which was

Table 4. Average values of soil and light characteristics from different sites and locations on the dunes.

Site	Location	PAR	CC	VWC_{av}	VWC_{spr}	VWC_{sum}	VWC_{aut}	pH_{H2O}	EC	O	A	N_{total}	P	K	Ca	Mg
Site 1	Bottom	553.4^{ab}	0.4^{a}	10.2^{b}	4.5^{b}	10.2^{b}	15.9^{a}	4.3^{a}	150.5^{a}	6.8^{a}	3.4^{a}	0.30^{a}	20.4^{b}	84.9^{b}	342.6^{a}	100.8^{a}
Site 1	Slope	439.8^{a}	0.7^{b}	9.0^{ab}	4.9^{b}	8.6^{ab}	13.6^{a}	4.3^{a}	152.0^{a}	10.4^{a}	0.2^{a}	0.26^{a}	14.7^{ab}	68.3^{ab}	343.4^{a}	88.5^{a}
Site 1	Top	808.4^{b}	0.8^{ab}	5.4^{a}	1.5^{a}	4.5^{a}	10.3^{a}	4.4^{a}	126.7^{a}	8.0^{a}	0.0^{a}	0.13^{a}	5.9^{a}	29.7^{a}	204.9^{a}	40.9^{a}
Site 2	Bottom	272.1^{a}	0.3^{ab}	9.0^{b}	5.1^{b}	8.2^{c}	13.7^{b}	3.9^{a}	207.0^{b}	9.0^{a}	2.0^{a}	0.21^{b}	19.8^{ab}	62.3^{a}	238.4^{b}	60.7^{b}
Site 2	Slope	503.9^{a}	0.4^{b}	5.8^{a}	2.3^{a}	5.1^{b}	10.1^{a}	4.2^{b}	149.2^{a}	4.0^{a}	1.5^{a}	0.11^{a}	11.1^{a}	30.1^{a}	111.1^{a}	14.7^{a}
Site 2	Top	381.5^{a}	0.2^{a}	4.7^{a}	3.7^{ab}	2.9^{a}	7.6^{a}	4.4^{b}	136.2^{a}	8.0^{a}	0.3^{a}	0.12^{ab}	29.3^{b}	29.6^{a}	160.7^{ab}	26.6^{ab}
Site 3	Bottom	482.5^{a}	0.6^{a}	26.6^{b}	26.6^{b}	23.2^{b}	30.0^{b}	4.0^{a}	319.2^{b}	9.0^{a}	0.0^{a}	1.00^{b}	68.6^{a}	161.1^{a}	459.9^{a}	261.7^{a}
Site 3	Slope	379.4^{a}	0.6^{a}	9.3^{a}	6.7^{a}	7.5^{a}	13.7^{a}	4.6^{b}	141.3^{a}	8.5^{a}	0.7^{a}	0.25^{a}	30.1^{a}	84.6^{a}	258.2^{a}	73.9^{a}
Site 3	Top	271.3^{a}	0.5^{a}	7.3^{a}	4.3^{a}	6.1^{a}	11.6^{a}	4.2^{ab}	156.8^{a}	8.3^{a}	0.0^{a}	0.16^{a}	21.3^{a}	43.5^{a}	206.9^{a}	40.6^{a}
Site 4	Bottom	245.8^{a}	0.4^{a}	8.7^{b}	4.4^{ab}	8.2^{a}	13.5^{ab}	4.4^{a}	90.4^{a}	12.3^{b}	0.0^{a}	0.32^{a}	30.2^{a}	96.0^{a}	285.6^{b}	78.7^{a}
Site 4	Slope	344.7^{a}	0.5^{b}	9.1^{b}	4.4^{b}	8.0^{a}	14.9^{b}	4.8^{a}	101.7^{a}	8.8^{a}	2.7^{a}	0.17^{a}	16.5^{a}	52.7^{a}	145.3^{a}	32.4^{a}
Site 4	Top	372.1^{a}	0.6^{c}	6.6^{a}	1.6^{a}	6.6^{a}	11.6^{a}	4.5^{a}	115.2^{a}	9.0^{ab}	0.0^{a}	0.29^{a}	26.2^{a}	89.0^{a}	211.4^{ab}	60.5^{a}

^{a}, ^{b}, ^{c} – indicate statistically important differences between locations at $p < 0.05$

Photosynthetically active radiation (PAR, µmol m^{-2} s^{-1}); canopy cover (CC); average, spring, summer and autumn soil volumetric water contents (VWC_{av}, VWC_{spr}, VWC_{sum}, VWC_{aut}, respectively, %); soil pH in water solution (pH_{H2O}); electrical conductivity (EC, µS); different soil horizon thicknesses (O – litter horizon and A – humus horizon, cm); and contents of total nitrogen (N_{total}, %), phosphorus (P, mg kg^{-1}), potassium (K, mg kg^{-1}), calcium (Ca, mg kg^{-1}) and magnesium (Mg, mg kg^{-1})

44% lower than the vegetation period average, whereas the summer soil moisture was 11% lower than the vegetation period average. Seasonal features showed significant differences with respect to location and site (Table 4).

The average pH_{H2O} was 4.3, with a minimum value of 3.4 and a maximum of 5.7 for all sites. At sites 2 and 3 the soil pH at the bottoms of the dunes was significantly lower compared with that of the slopes of the dunes (Table 4). No significant differences were observed at sites 1 and 4 regarding soil pH. Soil EC was used to obtain information about soil properties that induce plant growth. The average EC for dunes was 151.3 µS; the maximum value was 724.3 µS, and the minimum was 55.4 µS. According to the comparison analysis, the EC values were significantly higher at the bottoms of the dunes at sites 2 and 3 (Table 4). The average nitrogen content was 0.28%; the average at the tops of dunes was 0.17%, on the slopes was 0.20% and at the bottoms 0.46%. The total nitrogen content was significantly higher at the bottoms than on the slopes at site 2 and on the slopes and top at site 3; there were no significant differences recorded between locations at site 1 and 4 (Table 4). The average phosphorus content in the dune soils was 24.3 mg kg^{-1}; the phosphorus content was 20.7 mg kg^{-1} at the tops of the dunes, 18.1 mg kg^{-1} on the slopes and 34.2 mg kg^{-1} at the bottoms. Phosphorus content showed significant differences between locations only at higher dunes (Table 4). The average potassium content was 68.6 mg kg^{-1}, average Ca content was 244.2 mg kg^{-1} and average Mg 72.3 mg kg^{-1}.

The average PAR at midday in the fixed dune forests was 450 µmol m^{-2} s^{-1}. Significant differences based on location on dune were revealed at site 1 (Table 4). Canopy cover values varied between 0.1 to 0.8 and the average value was 0.5. At site 1, the bottoms and slopes showed significant differences in canopy cover, at site 2 slopes and top showed significant differences and at site 4 all locations differed from each other (Table 4).

The results of the linear mixed model showed that vascular plant species richness in the quadrats was affected by zone, aspect of the quadrat, light conditions (PAR), average pH, average soil water content, and total nitrogen and potassium contents (Table 5). The same factors significantly affected the total cover of vascular plants, with the exception of light conditions and the aspect of the quadrat, which exhibited no significant effects. In addition, the total cover was affected by the absolute height of the quadrat and by the thickness of the litter horizon.

The NMDS analysis of vascular plant species data resulted in a stress value of 0.208 (stress type 1). The NMDS analysis indicated that the most important factors ($p \leq 0.005$) controlling vascular plant species composition in the dune forests included site; the absolute height of the sample plot; canopy cover; the aspect of the quadrat; total bryophyte and lichen cover; and soil nitrogen, potassium and phosphorus contents (Fig. 4 and Table 6).

Table 5. Significance (p-values, type 3 effects) of factors contributing to species richness and the coverage of vascular plants according to a linear mixed model.

Species richness of vascular plants	DF	F-value	p-value
Location on dune (zone)	215.97	15.43	<0.001
Aspect of the quadrat	7.87	16.67	<0.001
Absolute height	183.53	0.17	0.685[a]
Cover of bryophyte and lichen layers	215.42	0.003	0.960[a]
PAR	215.18	15.46	<0.001[a]
VWC	216.36	26.54	<0.001
pH	216.54	10.70	0.001
N_{total}	215.46	29.22	<0.001[a]
P	216.92	0.002	0.969
K	216.85	4.98	0.027
O horizon	215.50	1.97	0.162
Total cover of vascular plant species	**DF**	**F-value**	**p-value**
Location on dune	102.68	13.46	<0.001
Aspect of the quadrat	3.29	1.53	0.356
Absolute height	2.31	22.06	0.032
Cover of bryophyte and lichen layers	199.17	1.86	0.174[a]
PAR	216.78	0.04	0.844
VWC	205.64	22.96	<0.001
pH	124.85	4.78	0.031[a]
N_{total}	217.00	27.28	<0.001[a]
P	32.27	0.12	0.727
K	139.17	24.43	<0.001
O horizon	174.46	6.61	0.011

[a] – indicates a negative effect

PAR = below-canopy photosynthetically active radiation (μmol m^{-2} s^{-1});
VWC = average soil volumetric water content (%);
pH = average pH_{H2O};
O = soil litter horizon thickness (cm);
N_{total} = nitrogen content (%);
P = phosphorus content (mg kg^{-1});
K = potassium content (mg kg^{-1})

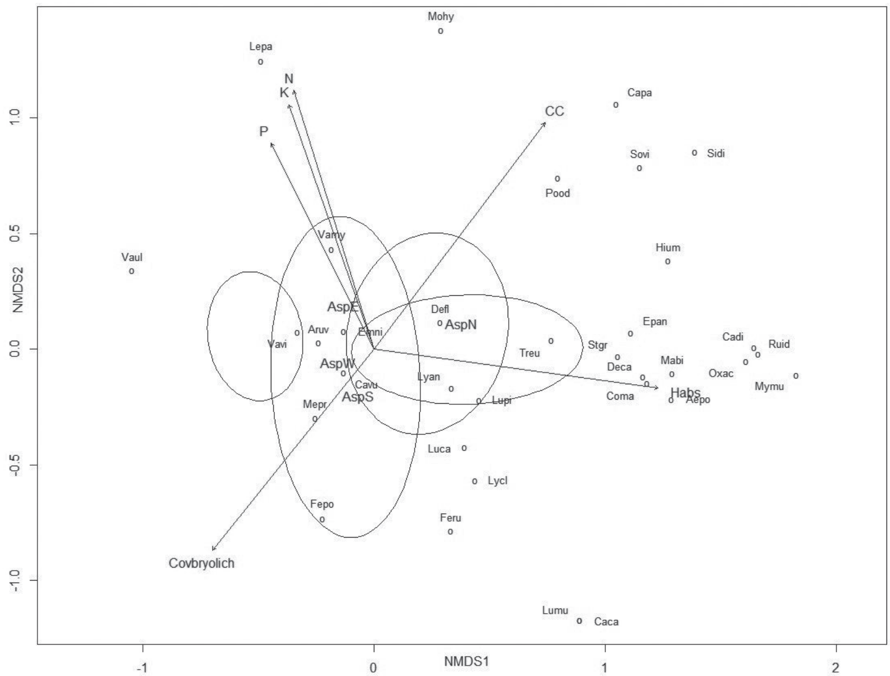


Fig. 4. Non-metric multidimensional scaling (NMDS) ordination graph with fitted environmental variables. Arrows represent environmental variables that were most significantly ($p \leq 0.005$) related to ordination.

Ellipses indicate sites. The environmental factors are as follows:

N = nitrogen content (%);
P = phosphorus content (mg kg^{-1});
K = potassium content (mg kg^{-1});
Habs = absolute height (m);
CC = canopy cover;
Asp = aspect of the quadrat;
Covbryolich = total coverage of bryophytes and lichens (%).

The list of species is as follows: Aepo = *Aegopodium podagraria*; Aruv = *Arctostaphylos uva-ursi*; Cavu = *Calluna vulgaris*; Capa = *Campanula patula*; Caca = *Carex caryophyllea*; Cadi = *Carex digitata*; Coma = *Convallaria majalis*; Deca = *Deschampsia caespitosa*; Defl = *Deschampsia flexuosa*; Emni = *Empetrum nigrum*; Epan = *Epilobium angustifolium*; Fepo = *Festuca polesica*; Feru = *Festuca rubra*; Hium = *Hieracium umbellatum*; Lepa = *Ledum palustre*; Luca = *Luzula campestris*; Lumu = *Luzula multiflora*; Lupi = *Luzula pilosa*; Lyan = *Lycopodium annotinum*; Lycl = *Lycopodium clavatum*; Mabi = *Maianthemum bifolium*; Mepr = *Melampyrum pratense*; Mohy = *Monotropa hypopitys*; Mymu = *Mycelis muralis*; Oxac = *Oxalis acetosella*; Pood = *Polygonatum odoratum*; Ruid = *Rubus idaeus*; Sidi = *Silene dioica*; Sovi = *Solidago virgaurea*; Stgr = *Stellaria graminea*; Treu = *Trientalis europaea*; Vamy = *Vaccinium myrtillus*; Vaul = *Vaccinium uliginosum*; Vavi = *Vaccinium vitis-idaea*.

Table 6. Relationships between species composition (non-metric multidimensional scaling (NMDS) ordination, Fig. 4) and environmental variables on dunes. Bold values are variables presented as arrows in Fig. 4.

Variable	r^2	p-value	Level of significance
H_{abs}	0.2541	**0.001**	***
CC	0.2486	**0.001**	***
$Cov_{bryolich}$	0.2054	**0.001**	***
Site	0.2949	**0.001**	***
N_{total}	0.2259	**0.002**	**
Asp	0.1552	**0.003**	**
K	0.2067	**0.004**	**
P	0.1634	**0.005**	**
Mg	0.1826	0.007	**
VWC_{aver}	0.1553	0.008	**
pH	0.1248	0.022	*
Ca	0.1180	0.030	*
H_{rel}	0.0942	0.062	.
EC	0.0809	0.073	.
Degr	0.0622	0.158	
Loc	0.0497	0.225	
O	0.0150	0.655	
A	0.0103	0.744	
PAR	0.0026	0.914	

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

H_{abs} = absolute height of the quadrat location (m);
CC = average canopy cover;
$Cov_{bryolich}$ = total coverage of bryophytes and lichens (%);
N_{total} = average total nitrogen content (%);
Asp = aspect of the quadrat;
K = average potassium content (mg kg^{-1});
P = average phosphorus content (mg kg^{-1});
Mg = average magnesium content (mg kg^{-1});
VWC_{aver} = average soil water content (%);
pH = average soil pH_{H2O};
Ca = average soil calcium content (mg kg^{-1});
H_{rel} = relative height (m);
EC = electrical conductivity (µS);
Degr = degree of inclination or ascent;
Loc = location on dune (bottom, slope, top);
O = average litter horizon thickness (cm);
A = average humus horizon thickness (cm);
PAR = average photosynthetically active radiation (µmol m^{-2} s^{-1})

4 Discussion

The most represented family on the studied dunes was the Poaceae with four species, followed by the Asteraceae with three species. These results are similar to those of Ruocco et al. (2014), who reported that the same families were most abundant on Mediterranean dunes. According to the MRPP test, ground vegetation zonation was prevalent on the studied dunes, with indicator species present for all zones. The zonation of ground vegetation is characteristic for dunes (Isermann 2005; Mandre et al. 2006; Tilk et al. 2011). *V. myrtillus* had the highest indicator value for the bottoms of the dunes and *C. vulgaris* for the tops. Only three species were determined to be indicators for the slopes of the dunes. This is because the species composition on the slopes involved species from bottoms and tops; therefore, the slopes can be considered transition zones.

The determination of factors that control the distribution patterns of plant communities remains a central goal in ecology studies. Species composition and community structure in dune forests is regulated by a variety of environmental factors. Based on the NMDS analysis, the most significant factors influencing species composition in the studied dunes were related to the site, such as absolute height, aspect and canopy cover of the quadrat, and its soil fertility, such as soil total nitrogen, potassium and phosphorus content. The most relevant ($p<0.001$) environmental variables influencing vascular plant species richness according to the model were quadrat location and aspect on the dune, the amount of PAR, soil volumetric water and total nitrogen content. This finding was in accordance with that of Pausas (1994), who concluded that main species richness determinants in forests are solar radiation, altitude, soil nitrogen content and soil moisture.

In dune areas, topography plays an important role in soil development and therefore affects the variability and distribution of vegetation (Jenny 1941; Sewerniak et al. 2017). Slope aspect also has strong effects on vegetation in large-scale relief forms, but slope aspect also is an important factor of inland dunes. North-facing slopes receive less solar radiation; these slopes have higher moisture contents, lower temperature and higher fertility (Huang et al. 2015; Sewerniak 2016). Both the model and the NMDS analysis confirmed that the aspect of the quadrat and the direction of transect had major influences on vascular plant species richness and composition, whereas vascular plant species cover was unaffected by the aspect of the slope and quadrat. Just as the aspect of the dune slope is important, the quadrat location on the dune is also highly important. Our results showed that species richness and cover were affected by location. Low-situated soils on the bottoms of dunes are characterised by much higher fertility and soil water content compared with those of the slopes and tops of the dunes, which are usually dry and infertile; similar conclusions were made by Örd (1972), Sewerniak (2016) and Sewerniak et al. (2017). The dominant soil type of the studied dunes was a Haplic Podzol, which is usually acidic, with a pH in the range of 4–5; the activity of microfauna is disrupted, which interferes with plant nutrition, especially the nitrogen supply to plants (Lõhmus 2004). Soil type and slope position affect soil fertility and therefore affect ground vegetation abundance, composition and diversity (Hart and Chen 2006; Tilk et al. 2011). The average pH of the studied dunes was 4.3, which is slightly lower than a pH value of 5.0 reported by Mandre et al. (2006) in the same dune area. In our study, the soil pH varied by nearly two units, possibly due to the relatively low vegetation cover and the rather high diversity of vegetation, as suggested by Isermann (2005). Soil reaction significantly influences the mineral nutrition of plants by directly or indirectly altering the availability of mineral nutrients to plants (Klõšeiko 2003; Marschner 2012). Our model results showed that an increase in soil pH resulted in higher numbers of vascular plant species but negatively affected vascular plant species coverage. Similar conclusions were reported by Grime (1973), who reported that the maximum numbers of species in unmanaged grassland occur at a soil pH of 6.1–6.5; only a few species are adapted to exploit highly acidic soils. Also, according to the NMDS, species composition moderately depended on soil pH. One method for obtaining information about soil nutritional status is to evaluate EC; in the current study, significant differences were between the tops and bottoms and between the slopes and bottoms of dunes at sites 2 and 3; sites 1 and 4 showed no significant differences concerning soil EC based on location. However, according to the NMDS analysis, electrical conductivity may be irrelevant.

The well-known pattern that species richness peaks at intermediate levels and starts to decline at higher nutrient levels (Grime 1979) has also been demonstrated in dune areas (Lichter 1998). The results of the current study also confirm this statement: according to the model, higher total nitrogen content significantly reduces species richness. In addition, the NMDS analysis indicated that nitrogen was a statistically important factor for modelling vascular plant species composition on dunes. In contrast to the effect of nitrogen, the concentrations of potassium positively affected vascular plant species richness and coverage according to model. The NMDS also indicated potassium and phosphorus as variables that significantly affect species composition, whereas the effects of calcium and magnesium were less significant in shaping species composition, although calcium is often among the most important exchangeable cations in the growth substrate and can affect the availability of other nutrients (Pausas and Austin 2001).

Light is the most important environmental factor affecting ground vegetation (Reich et al. 2012; Márialigeti et al. 2016). The results of current study showed that more light reduced the number of vascular plant species in dune forests. We can assume that on dunes, ground vegetation is stressed, and an increase in one stress factor decreases the number of different vascular plant species and may increase the occurrence of specific cryptogams (Košuthová et al. 2015). Separating the effect of light from the availability of water to vascular plants is complicated, as solar radiation affects both soil temperature and soil moisture, which, in turn, affect soil chemical properties (Bravo et al. 2011). Our model indicated that while increased light reduced species richness, the increase in volumetric water content increased species richness and also positively affected the cover of vascular plants. Dunes are presumed to be highly limited by water stress because of their sandy texture (Martinez and Psuty 2004). High topographical heterogeneity of dunes leads to the formation of microhabitats with different soil water conditions. In this respect, we should not underestimate the interaction between soil water content and ground vegetation, as dense ground vegetation can affect soil moisture content, which was also reported by both Liu et al. (2010) and Zheng et al. (2015). According to our results, in the spring, soil moisture was statistically lower compared to summer and autumn measurements. Ground vegetation in the spring is sparse and therefore unable to contain moisture in the soil, but in the summer and autumn, when vegetation is thicker and in full growth, soil moisture is influenced by ground vegetation coverage.

According to our hypothesis, ground vegetation forms different vegetation zones and patches; species composition at the bottoms of dunes differed significantly from that of other locations, not only on the higher dunes but also on the lower dunes. However, between slopes and tops, no significant differences were recorded; only at the highest site 2 there was significant difference in species composition. Therefore, we can conclude that complex growth conditions at the bottoms of the dunes are markedly different compared with those on the slopes and at the tops of dunes even on relatively low dunes, resulting in substantially different vascular plant species richness and composition.

In conclusion, factors affecting vascular plant species richness, composition and horizontal structure are related to dune topography, leading to the differentiation of soils and therefore complexes of different microhabitats that are populated by various vascular plant species.

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Effect of environmental factors on the composition of terrestrial bryophyte and lichen species in Scots pine forests on fixed sand dunes

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Abstract
Aim of the study: To investigate terrestrial bryophyte and lichen species richness and environmental factors affecting the composition of species.
Area of the study: Four Boreal zone fixed dunes were selected in the coastal area of the Baltic Sea in southwest Estonia.
Material and methods: Non-metric multidimensional scaling was performed to analyse distribution patterns and environmental factors like canopy cover, photosynthetically active radiation, soil organic horizon thickness and decomposition rates, soil volumetric water content, soil pH and electrical conductivity and soil nutrients correlated with bryophyte and lichen species composition.
Main results: Thirty bryophytes and 22 lichens were found on 232 sample plots, the most frequent species were *Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp., *Dicranum polysetum* Sw. ex anon., *Cladonia arbuscula* (Wallr.) Flot. and *Cladonia furcata* (Huds.) Schrad. The lichen species richness was highest on the slopes of the

dunes and decreased towards the bottoms and tops; bryophyte species richness was higher on the bottoms and decreased towards the tops of the dunes.
Research highlights: The composition of bryophytes and lichens is significantly influenced by the aspect and the location on the dune, light conditions, soil pH, soil salinity (measured as electrical conductivity) and volumetric water content, thickness of moderately decomposed organic horizon and vascular plant species cover.

Keywords
Inland dunes; terrestrial bryophyte and lichen communities; environmental factors; topography.

Introduction

During the last century in Europe, mainly due to urbanization and other human-related factors, a reduction of about 70% of the dune systems has been estimated (Mc Lachlan & Brown, 2006). Vegetated dunes are complicated and fragile ecosystems which have a very high ecological and conservative value (Lemauviel *et al*., 2003; Van der Maarel, 2003). Lichens and bryophytes have principal functional importance on boreal zone inland dune forests (Ahti & Oksanen, 1990); bryophytes dominate the forest floor vegetation and play an important role in the water and carbon budgets and improve microenvironment (Bond-Lamberty & Gower, 2007; Márialigeti *et al*., 2016) while lichens colonize open sand surfaces and create suitable conditions for vascular plants (Ketner-Oostra & Sykora, 2000). Maintenance of biodiversity is an integral part of sustainable forest management which is a desirable goal for most forest-related initiatives and legislative bodies. Assessment of biological diversity is essential for understanding forest ecology and measuring sustainable forest management binds conservation and enhancement of biological diversity (MCPFE Liaison Unit Vienna, 2002; Canullo *et al*., 2013). According to Pharo *et al*. (1999) the bryophytes and lichens have different patterns of diversity compared to vascular plant species and therefore management practices and conservation actions should take into account the specialty.

Multiple studies have been conducted to clarify lichen and bryophyte distribution and richness and to give insight into the different factors that influence their growth in forests. These factors include substrate availability (Pharo *et al*., 1999; Ingerpuu, 2002), litter composition and quality (Hill, 1979; Magnusson, 1982;), soil nutrients (especially magnesium) and acidity (pH) (Oechel & Van Cleve, 1986; Pausas, 1994; Jun & Rozé, 2005; Kösta & Tilk, 2008; Košuthovà *et al*., 2015; Jüriado *et al*., 2016), light conditions and soil moisture (Ketner-Oostra & Sykora, 2000; Márialigeti *et al*., 2016) and the cover of vascular plant species (Löbel *et al*., 2006). Also, studies have pointed out stress and disturbance as important factors affecting cryptogam communities (Forey *et al*., 2008; Cogoni *et al*., 2011; Ciccarelli, 2015).

Topographical factors, especially the height and slope aspect, have been modestly discussed when bryophytes and lichens are concerned, whereas for the vascular plant species richness and composition the slope effect has been considered as an important factor (Jenny, 1941; Sewerniak, 2016; Sewerniak *et al*., 2017; Tilk *et al*., 2017). In northern hemisphere north-facing slopes receive six times less solar radiation compared to south-facing slopes and therefore microclimatic conditions on the slopes vary greatly (Auslander *et al*., 2003; Mandre *et al*., 2008; Sewerniak *et al*., 2017; Sewerniak & Jankowski, 2017). Therefore, a respective variation in the species richness and composition of the understory vegetation can be expected as well (Solon *et al*., 2007; Sewerniak & Jankowski, 2017). Previous studies have provided data for the zonation of the vascular plant species composition along the dune profile (Zoladeski, 1991; Sewerniak & Jankowski, 2017; Tilk *et al*., 2017); however, precise information is insufficient for lichens and bryophytes. Besides, thorough knowledge of the abundance of lichens and bryophytes, as well as on topographical and environmental factors that affect their patterns in forests on fixed dunes, is still lacking.

This paper is continuation of earlier works of Tilk *et al*. (2011; 2017), where the vascular plant species richness and environmental factors were investigated. The main aim of this paper is to describe the variability of the bryophyte and lichen layer on *Pinus sylvestris* dominated fixed dunes and to give a new insight into specific environmental and topographical factors that influence bryophyte and lichen communities and species distribution. The specific objectives of the study were (1) to determine if bryophyte and lichen species richness varies along the topographical gradient on dunes; (2) to study whether zoning of the bryophyte and lichen species composition along the dune profile is possible; (3) to analyse the variability of bryophyte and lichen species in dune forests based on ecological indicator values (Düll, 1991; Wirth, 2010); and (4) to analyse the influence of environmental and topographical factors on the composition of the bryophyte–lichen layer.

Material and Methods

Study area

The investigated dune system is situated in Southwest Estonia, in the coastal area of the Baltic Sea (Fig. 1). The dunes are located on the Uulu-Võiste landscape protection area and on the Luitemaa nature reserve where, the following priority habitats according to Council Directive 92/43/EEC (1992), are protected: wooded dunes of the Atlantic, Continental and Boreal region (type 2180), Western Taïga (type 9010), Fennoscandian deciduous swamp woods (type 9080), fixed coastal dunes with herbaceous vegetation (grey dunes) (type 2130) and humid dune slacks (type 2190).

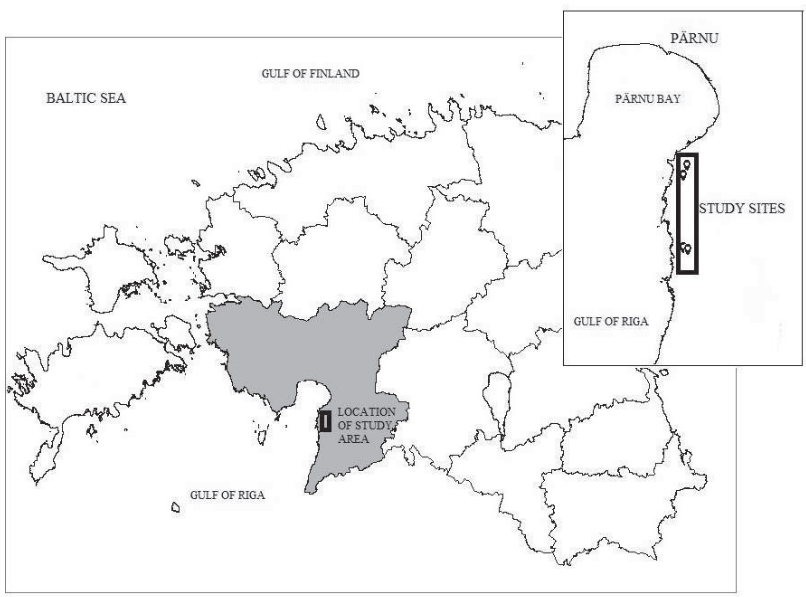

Figure 1. Location of study area and study sites in Estonia

For the investigation of bryophyte and lichen flora on wooded dunes of different height, four sampling sites were selected (Table 1). Sampling sites distance to Baltic Sea (Pärnu Gulf) is ranging between 2 and 3 km.

Table 1. Study sites, number and direction of quadrats.

Site No.	Coordinates	Absolute height of the dune (m.a.s.l)	Relative height of the dune (m)	No. of quadrats on the dune	Direction of the transect
Site 1	58º8´20”N 24º30´27”E	28	16	58	S->N
Site 2	58º8´23“N 24º30´36“E	33	21	108	W->E
Site 3	58º14´28“N 24º31´21“E	12	6	32	S->N
Site 4	58º13´51“N 24º30´47“E	10	6	34	W->E

According to information from State Forest Management Centre database the dunes belong to the *Cladonia* and *Vaccinium vitis-idaea* forest site type, where the average stand age is 195 years; the average stand canopy cover is 55%; the average height of pines is 23 m; the site quality index is IV and the density of the understorey is low.

According to the closest weather station of the Estonian Weather Service in Pärnu, the main climate characteristics during the period of our investigations in 2010 were as follows: average annual temperature 5 ºC with maximum average of 21.8 ºC in July and minimum average of -12.3 ºC in January; total average precipitation 908 mm with maximum of 122.8 mm in August and minimum of 27 mm in January.

Mean relative air humidity was 84% in the area. The length of the thermal growing period (mean temperature above 5 ºC) was 203 days (from 25.04.2010 to 14.11.2010). During the winter of 2009/2010 there was permanent snow cover recorded of 112 days (11.12.2009 — 01.04.2010) and throughout winter there was altogether 143 days with snow.

Methods

Field studies on four *Pinus sylvestris* dominated dunes were carried out in July 2010 for bryophyte and lichen species determination. On every dune, quadrats with the size of 1 m^2 formed a continuous transect over the dune, starting from the bottom in front of the dune and moving over the top to the bottom beyond with the distance of one meter between the quadrats (n = 232). Additional quadrats (n = 464) to determine species that did not occur on the basic quadrats of the transect were placed one meter to the left and one meter to the right of the basic quadrat. Data about species found on the additional quadrats were added into overall species list but were not included into the further statistical analysis.

On every quadrat, the total cover of the bryophyte and lichen layer, the total cover of vascular plants and the cover of each bryophyte and lichen species were estimated visually, using the scale 1—100%. Dominant species were determined based on Braun-Blanquet five-point cover-abundance scale: 5 — very abundant; 4 — abundant; 3 — plentiful; 2 — sparsely; 1 — single. The individuals that could not be identified in the field were collected and determined in the laboratory; species identification included using the Tallinn Botanical Garden bryophyte and lichen herbarium for comparative analysis. The nomenclature of lichens and bryophytes follows Randlane *et al*. (2016) and Ingerpuu *et al*. (1998) respectively.

On every quadrat, canopy cover was assessed visually by two evaluators as a measure of the percentage of forest floor covered by a vertical projection of the tree canopies expressed at scale 0 to 1 (Masing, 1979; Pihelgas, 1983). Below-canopy photosynthetically active radiation

(PAR, μmol $m^{-2}s^{-1}$) was measured (n =10 per quadrat) with light interception device AccuPAR (Model PAR-80) in 23 of July 2008 at midday full sunshine. As light is highly variable, measurements were performed simultaneously during a very short time period (from 11:00 to 13:00) at all sites.

Absolute heights (meters above sea level, m.a.s.l) and aspects of the quadrats on the dune slopes (N; S; E; W) were determined using Garmin GPSMap 76CSx device and relative heights were calculated using the first quadrat on the bottom of the dune as a zero. An inclinometer was used to assess the incline of slopes and quadrats were classified into five groups according to angle value: 1 (1 — 10 degrees); 2 (11 — 20 degrees); 3 (21 — 30 degrees); 4 (31 — 40 degrees) and 5 (41 — 50 degrees).

Soil organic horizon (O-horizon) thickness and its decomposition rates: 1 — poorly decomposed (O_i) sub-horizon; 2 — medium decomposed (O_e) sub-horizon and 3 — well decomposed (O_a) sub-horizon, were assessed.

Volumetric water content (VWC, %) in the soil was determined in every quadrat with Field Scout™ TDR 300 at a depth of 20 cm (n = 3). The data were collected in May, July and September 2008 and there was no rain recorded at least 3 days before measurements. Soil samples of every quadrat were collected in July 2010 from a depth of 20 cm from ground level (for measuring soil pH and electrical conductivity). Soil pH and electrical conductivity were measured from a soil-distilled water mixture (1:2.5 or for samples with high organic matter 1:5) with Eutech Instruments PC300 pH/conductivity meter.

Soil samples from mineral topsoil for analysing nitrogen (N), phosphorous (P), potassium (K), calcium (Ca) and magnesium (Mg) content were collected from a depth of 20 cm (n = 15 per site) on the bottoms, slopes and tops of the dunes. The results are presented as N: P; N: K and Ca: Mg ratios and absolute values are presented in an article by Tilk *et al*. 2017. The concentrations of N, P, K, Ca and Mg in the mineral topsoil samples (n = 60) were determined in the Laboratory of Plant Biochemistry of the Estonian University of Life Sciences. The soil samples were analysed for their extractable concentration of P (ammonium lactate; by FiaStar5000 (Flow Injection Analyser)), K (ammonium lactate; Flame Photometric Method), Ca (ammonium acetate: Flame Photometric Method), Mg (ammonium acetate; by FiaStar5000 (Flow Injection Analyser)) and for total concentration of N (Copper Catalyst Kjeldahl Method).

Data analysis

Bryophytes and lichens were grouped based on the ecological indicator values of species according to Düll (1991) and Wirth (2010).

For statistical analysis, quadrats were grouped according to location based on the relative height and the angle of the quadrat as follows: bottom (n = 52 quadrats), slope (n = 142 quadrats) and top (n = 38 quadrats). Correlation analysis was performed with Microsoft Excel 2010 to determine relations between canopy cover and some topographical variables with the precondition of checked data normality. To clarify significant differences between groups one-way ANOVA of multiple groups followed by post-hoc Tukey HSD test using Tukey-Kramer formula for unequal observations was performed (Vasavada, 2016).

A linear mixed model using free statistical software R Version 3.2.3 (R Core Team, 2015) function “lmer” in package lme4 (Bates *et al.*, 2015) (with a site as a random factor) was applied to clarify the effect of location on environmental factors and cryptogams characteristics. If a statistically significant effect of location was observed, a Tukey HSD test was applied to compare the group means. A level of significance of α = 0.05 was used to reject the null hypothesis after statistical tests.

The effect of grouping factors on bryophyte and lichen data was tested using Multiple Response Permutation Procedure (MRPP) (Mielke *et al*., 1976). To correct the p-values for multiple comparisons in MRPP, Bonferroni correction was applied. Indicator species analysis

(ISA) was conducted to specify indicator species for different zones (Dufrene & Legendre, 1997). The statistical significance of indicator values was proven using Monte Carlo simulation. MRPP and ISA were performed with PC-ORD Version 6 (McCune & Mefford, 2011).

To analyse species distribution patterns and environmental variables correlated with bryophyte and lichen species composition, non-metric multidimensional scaling (NMDS) with free statistical software R Version 3.2.3 (R Core Team, 2015) in the community ecology package Vegan (Oksanen *et al*., 2016) was performed. NMDS was run using the function "metaMDS" (default settings) and Bray-Curtis dissimilarities. For fitting environmental vectors and factors onto ordination, function "envfit" was used (Oksanen, 2015).

The analyses of species composition (MRPP and NMDS) were performed twice: 1) based on the abundance data of bryophytes and lichens; 2) based on the abundance data of bryophytes. Separate analysis based on lichen data was not performed, as lichens were present on only 22% of the studied quadrats.

Results

Environmental factors

Soils are Haplic Podzols with A-horizon on the bottoms and Haplic Podzol on the slopes and on tops of the dune. Average values for light conditions and soil characteristics are presented in Table 2. Canopy cover showed a negative correlation (r = -0.67) with the aspect of the quadrat, being higher on the northern and eastern quadrats and lower on southern and western quadrats. Canopy cover was significantly higher on the slopes (Table 2), while PAR showed no significant differences between locations on dunes. In addition, significant differences were found for soil volumetric water content (VWC), pH_{H2O} and electrical conductivity between different locations (Table 2).

Table 2. Average values (±SE) for photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}), canopy cover, soil volumetric water content (VWC, %), pH, electrical conductivity (EC, μS cm^{-1}), average ratios of N:P, N:K and Ca:Mg and thicknesses of soil organic horizons with different decomposition rates (O_i — poorly decomposed; O_e — medium decomposed and O_a — well decomposed, cm) from different locations on the dunes according to linear mixed model. Letters denote significant differences between locations according to Tukey HSD test. Average values of soil and light characteristics from different locations on the dunes for each study site are presented in Tilk *et al*. 2017: table 4.

		Location on dune	
	Bottom	Slope	Top
PAR	420.4±64.2^a	440.4±54.5^a	431.1±70.0^a
Canopy cover	0.4±0.07^a	0.6±0.07^b	0.4±0.08^a
VWC	12.8±1.6^c	8.6±1.6^b	6.2±1.7^a
pH	4.2±0.1^a	4.4±0.1^b	4.4±0.1^b
EC	185.0±21.0^b	140.6±19.8^a	131.2±21.7^a
N:P	147.2±28.6^a	141.9±28.6^a	136.2±34.1^a
N:K	41.2±3.7^a	39.0±3.7^a	39.9±5.2^a
Ca:Mg	3.9±1.0^a	6.0±1.0^b	5.1±1.2^{ab}
O_i	2.8±0.4^a	2.6±0.4^a	2.7±0.5^a
O_e	5.3±0.9^a	4.5±0.9^a	5.7±1.1^a
O_a	1.0±0.7^a	0.9±0.7^a	0.0±0.8^a

Average soil VWC was highest on the bottoms of the dunes, being on average 48% higher compared to the top of the dunes. Average soil VWC on the north facing quadrats was significantly higher compared to the south, east and west facing quadrats ($p < 0.01$), while differences between soil volumetric water contents on the southern, western and eastern quadrats were not significant ($p > 0.05$).

Bottoms of the dunes also obtained higher electrical conductivity and lower soil pH values. The average values for N: P and N: K ratios were similar in all of the observed locations; only the Ca: Mg ratio showed statistically significant differences between bottoms and slopes (Table 2). Soil organic horizon averaged 9.1 cm on the bottom, 8 cm on the slope and 8.4 cm on the top of the dunes. The poorly decomposed organic layer made up 30.8% of the bottoms, 32.5% of the slopes and 32.1% of the tops of the dunes; the medium decomposed organic layer formed 58.2% of the bottoms, 56.3% of the slopes and 67.9% of the tops and the well decomposed organic horizon formed 11% of the bottoms, 11.3% of the slopes and was missing from the tops of the dunes.

Species richness and composition changes along topographical and environmental gradients

Altogether, 52 species of bryophytes and lichens were distinguished on the quadrats (30 species of bryophytes and 22 species of lichens). Bryophytes were present on all 232 quadrats while lichens were recorded on 50 quadrats. Six bryophyte species were common to all four dunes while 17 species were recorded only on one dune. The most frequent bryophyte species were *Pleurozium schreberi* (present on 90% of the quadrats), *Hylocomium splendens* (64%) and *Dicranum polysetum* (51%). None of the lichen species was recorded on all dunes; the most frequent lichen species, *Cladonia arbuscula* (present on 6% of the quadrats), was found on three dunes. Fourteen lichen species were recorded on only one dune. There were four species found on the additional quadrats: lichen *Cladonia cornuta* (L.) Hoffm. and bryophytes *Cephaloziella hampeana* (Nees) Schiffn., *Ptilidium pulcherrimum* (Weber) Vain. and *Scleropodium purum* (Hedw.) Limpr. *P. schreberi* dominated on 128 quadrats, *H. splendens* on 76 and *D. polysetum* on 11 quadrats. *Cladonia rangiferina* (L.) F.H. Wigg. (on four quadrats) was the only dominated lichen species more than once.

Average lichen species richness was the highest on the slopes of the dunes and decreased towards the bottoms and tops (Table 3). Bryophyte species richness was significantly higher on the bottoms of the dunes, decreasing towards the tops of the dunes. The cover of the bryophyte and lichen layer was remarkably higher on the tops, contrary to the cover of vascular plants, which was the highest on the bottoms of the dunes (Table 3).

Table 3. Average species richness for lichens (S_{Lichen}), bryophytes ($S_{Bryophyte}$), total cover of lichen and bryophyte layer ($Cover_{LichBryo}$) and total cover of vascular plant species layer ($Cover_{Vascular}$) (±SE) on different locations according to the linear mixed model. Letters denote significant differences between locations according to Tukey HSD test.

Location	S_{Lichen}	$S_{Bryophyte}$	$Cover_{LichBryo}$	$Cover_{Vascular}$
Bottom	$0.1±0.1^{a}$	$3.0±0.2^{b}$	$82.9±5.0^{ab}$	$63.2±4.7^{b}$
Slope	$0.5±0.1^{b}$	$2.6±0.1^{a}$	$80.3±4.6^{a}$	$39.1±4.0^{a}$
Top	$0.1±0.2^{a}$	$2.5±0.2^{a}$	$91.6±5.3^{b}$	$43.6±5.1^{a}$

According to the ecological indicator values (Düll, 1991), the highest number of bryophyte species were light-demanding species (with light value 8, 26% of all bryophyte species), while there were some (6% of bryophyte species) shade-tolerant species (Fig. S1 A [supplementary]). The moisture preference of bryophyte species was variable as the most frequent values of moisture index varied between 4 and 7, referring to the preference of moderately dry to moist habitats. Based on pH indices assigned to bryophyte species, the majority of species preferred acidic substrate; two species were with broad pH tolerance (Fig. S1 A [suppl.]).

Light index (according to Wirth, 2010) was not available for 36% of lichen species, however, according to available indices, lichens were mainly light-demanding species (the most frequent values of the light index were 7 and 8) (Fig. S1 B [suppl.]). Based on moisture and substrate pH indices, the highest number of lichen species was species with broad amplitude; however, it must be considered that moisture and substrate pH indices were unavailable for 8 lichen species in each case (Fig. S1 B [suppl.]).

According to the MRPP test based on zones on dunes, bryophyte and lichen communities were significantly different on the bottoms *versus* tops (p-value = 0.015) and slopes *versus* tops (p-value = 0.012) while bottoms and slopes showed no statistically significant differences (p-value = 0.535) (Table 4). When only bryophyte communities were concerned, slopes and tops were similar (p-value = 0.263), while bottoms *versus* slopes (p-value = 0.001) and bottoms *versus* tops (p-value = 0.002) showed statistically significant differences.

Table 4. The results of multiple response permutation procedure (MRPP) tests for the comparison of bryophyte and lichen species (p-value$_{bryolich}$) and bryophyte species (p-value$_{bryo}$) composition on different zones on dunes.

Test pair	Bottom *vs*. Slope	Bottom *vs*. Top	Slope *vs*. Top
p-value$_{bryolich}$	0.535	**0.015**	**0.012**
p-value$_{bryo}$	**0.001**	**0.002**	0.263

Bold values are significant after the Bonferroni correction

The distribution of bryophyte and lichen species in different locations on the dunes is shown in Table S1 ([suppl.]). Indicator species analysis based on bryophyte and lichen species data pointed out characteristic species for zones on dunes: *Brachythecium erythrorrhizon*, *Brachythecium oedipodium* and *Hylocomium splendens* for the bottoms, *Ceratodon purpureus*, *Cladonia rangiferina* and *Cladonia stygia* for the slopes of the dunes and *Pleurozium schreberi* for the tops.

Environmental factors affecting bryophyte and lichen species composition

NMDS analysis (Table 5) suggested that the most significant environmental factors (level of significance $p \leq 0.001$) affecting epigeic bryophytes and lichens were site-specific factors such as aspect and height of the quadrat, but also vascular plant cover, PAR, soil VWC, pH, electrical conductivity and thickness of O_e sub-horizon (Fig. 2).

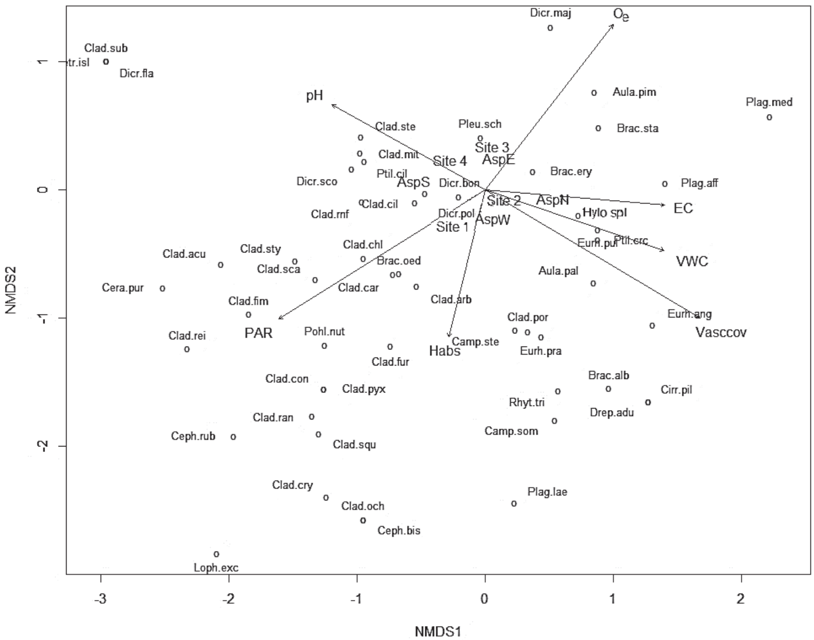

Figure 2. NMDS ordination (stress type 1), based on the abundance data of bryophytes and lichens. The arrows indicate environmental factors that were the most significantly ($p \leq 0.001$) related to the ordination (see also Table 5). Environmental factors: Habs = absolute height (m.a.s.l); Asp = aspect of the quadrat (S; N; E; W); EC = average conductivity (µS cm^{-1}); pH = average soil pH; VWC = average soil water content (%); PAR = photosynthetically active radiation (µmol $m^{-2}s^{-1}$); O_e = average thickness of moderate decomposed organic horizon layer (cm); Vasccov = cover of vascular plants. List of lichen and bryophyte species: Aula. pal = *Aulacomnium palustre*; Aula. pim = *Aulacomnium palustre var. imbricatum*; Brac. alb = *Brachythecium albicans*; Brac. ery = *Brachythecium erythrorrhizon*; Brac. oed = *Brachythecium oedipodium*; Brac. sta = *Brachythecium starkei*; Camp. som = *Campylium sommerfeltii*; Camp. ste = *Campylium stellatum*; Ceph. bis = *Cephalozia bicuspidata*; Ceph. rub = *Cephaloziella rubella*; Cera. pur = *Ceratodon purpureus*; Cetr. isl = *Cetraria islandica*; Cirr. pil = *Cirriphyllum piliferum*; Clad. arb = *Cladonia arbuscula*; Clad. cil = *Cladonia ciliata*; Clad. mit = *Cladonia mitis*; Clad. por = *Cladonia portentosa*; Clad. ran = *Cladonia rangiferina*; Clad. ste = *Cladonia stellaris*; Clad. sty = *Cladonia stygia*; Clad. acu = *Cladonia acuminata*; Clad. car = *Cladonia cariosa*; Clad. chl = *Cladonia chlorophaea*; Clad. con = *Cladonia coniocraea*; Clad. cry = *Cladonia cryptochlorophaea*; Clad. fim = *Cladonia fimbriata*; Clad. fur = *Cladonia furcata*; Clad. och = *Cladonia ochrochlora*; Clad. pyx = *Cladonia pyxidata*; Clad. rnf = *Cladonia rangiformis*; Clad. rei = *Cladonia rei*; Clad. sca = *Cladonia scabriuscula*; Clad. squ = *Cladonia squamosa*; Clad. sub = *Cladonia subulata*; Dicr. bon = *Dicranum bonjeanii*; Dicr. fla = *Dicranum flagellare*; Dicr. maj = *Dicranum majus*; Dicr. pol = *Dicranum polysetum*; Dicr. sco = *Dicranum scoparium*; Drep. adu = *Drepanocladus aduncus*; Eurh. ang = *Eurhynchium angustirete*; Eurh. pra = *Eurhynchium praelongum*; Eurh. pul = *Eurhynchium*

pulchellum; Hylo. spl = *Hylocomium splendens*; Loph. exc = *Lophozia excisa*; Plag. aff = *Plagiomnium affine*; Plag. med = *Plagiomnium medium*; Plag. lae = *Plagiothecium laetum*; Pleu. sch = *Pleurozium schreberi*; Pohl. nut = *Pohlia nutans*; Ptil. cil = *Ptilidium ciliare*; Ptil. crc = *Ptilium crista-castrensis*; Rhyt. tri = *Rhytidiadelphus triquetrus*.

When only bryophyte communities were concerned, NMDS analysis pointed to the aspect, vascular plant cover, PAR, canopy cover, thickness of O_e sub-horizon and soil VWC, pH, and electrical conductivity as the most significant factors (Table 5).

Table 5. Relationships between species composition (NMDS ordination, Fig. 2) and environmental factors on the dunes. H_{rel} — relative dune height (m); H_{abs} — absolute dune height (m.a.s.l); PAR — below-canopy photosynthetically active radiation (μmol $m^{-2}s^{-1}$); VWC_{aver} — soil volumetric water content (%); AvpH — average pH_{H2O}; EC — average electrical conductivity (μS cm^{-1}); Cancov — canopy cover; O_i — poorly decomposed soil organic horizon thickness (cm); O_e — medium decomposed soil organic horizon thickness (cm); O_a — well decomposed soil organic horizon thickness (cm); A — humic horizon thickness (cm); N — nitrogen content (%); P — phosphorus content (mg kg^{-1}); K — potassium content (mg kg^{-1}); Ca — calcium content (mg kg^{-1}); Vasccov — vascular plant species coverage (%); Loc — location on dune; Asp — aspect of the quadrat (N; S; E; W). sc significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'n.s.' not significant

Variable	Bryophyes and lichens			Variable	Bryophytes		
	R^2	*p*-value	sc		R^2	*p*-value	sc
Asp	0.1846	0.001	***	Asp	0.182	0.001	***
Vasccov	0.1715	0.001	***	Vasccov	0.1805	0.001	***
PAR	0.1616	0.001	***	PAR	0.146	0.001	***
O_e	0.1191	0.001	***	VWC_{aver}	0.1082	0.001	***
Site	0.1102	0.001	***	O_e	0.0939	0.001	***
VWC_{aver}	0.0971	0.001	***	AvCond	0.0934	0.001	***
AvCond	0.0891	0.001	***	AvpH	0.0821	0.001	***
AvpH	0.0837	0.001	***	Site	0.0703	0.002	**
H_{abs}	0.0626	0.001	***	Cancov	0.0592	0.001	***
H_{rel}	0.0445	0.004	**	H_{rel}	0.0489	0.005	**
Cancov	0.036	0.018	*	H_{abs}	0.0453	0.002	**
O_a	0.0343	0.025	*	K	0.0381	0.012	*
A	0.0298	0.033	*	Mg	0.0314	0.033	*
Loc	0.0297	0.012	*	A	0.0304	0.028	*
K	0.0295	0.033	*	P	0.028	0.044	*
P	0.0243	0.066	.	N	0.0272	0.058	.
Mg	0.0242	0.06	.	Loc	0.025	0.036	*
N	0.0229	0.063	.	Ca	0.0107	0.269	n.s.
O_i	0.0116	0.259	n.s.	O_a	0.0061	0.491	n.s.
Ca	0.007	0.434	n.s.	O_i	0.0009	0.898	n.s.
EA	0.0017	0.83	n.s.	EA	0.0003	0.97	n.s.

Discussion

Coastal sand dunes are one of the most threatened ecosystems in the world because of human activities and plant invasion (Cogoni *et al*., 2011; Vaz *et al*., 2014). Changes in traditional land use and invasions of non-native species affect the composition and structure of native vegetation and may lead to loss of biodiversity (Latorre *et al*., 2013; Rivis *et al*., 2016). Most of the Estonian coastal vegetation consists of semi-natural plant communities with moderate human management (Rivis *et al*., 2016). Lichens and bryophytes are considered to be pioneer species on open dune areas; they form habitats for other plants, collect humus and wither the substrate. They also play an important role in protecting the surface of the dunes from water and wind erosion (Cogoni *et al*., 2011) as well as provide stability, nutrients and moisture to the soil (Fernández & Barradas, 1997). Therefore, the significance of lichens and bryophytes on dunes should not be underestimated. In northern and boreal temperate zones, lichen-rich assemblages are restricted to edaphically specific stressful environments with nutrient insufficiency (Košuthovà *et al*., 2015).

In Estonia 594 species of bryophytes (according to Vellak *et al*., 2015) and 1176 species of lichens (according to Randlane *et al*., 2016) have been identified. In this study, a total of 30 species of epigeic bryophytes and 22 species of epigeic lichens were distinguished on the quadrats. In forests of the northern hemisphere, epigeic bryophyte communities are primarily dominated by a few common species with very broad ranges of tolerance such as *P. schreberi* (Frego, 2007). As regards this point, the dune forest in our study area is not an exception and *P. schreberi* was observed in 90% and *H. splendens* in 64% of the quadrats respectively. The species composition on Rannametsa dunes seems to have been quite stable over three decades as the most common species in our study were also mentioned by Örd (1972), who pointed out different *Cladonia* species and *Cetraria islandica* (L.) Ach. as the most common species in the same dune area. Two lichen species are according to the IUCN Red List near threatened (NT) and vulnerable (VU) in Estonia: *Cladonia portentosa* (Dufour) Coem. (NT) and *Cladonia scabriuscula* (Delise) Nyl. (VU).

Soil and vegetation units of the coastal landscape in Estonia strongly depend on the topography, geological structure and water regime (Rivis *et al*., 2016). Haplic Podzols, characteristic of Estonian coastal areas, are nutrient-poor soils. The most important plant growth-limiting elements in the terrestrial ecosystems are nitrogen and phosphorus (Güsewell, 2004). The high value of the N: P ratio indicates P limitation in the observed dune sands. Our results showed that the N: P and N: K ratios did not differ between the different locations. Only the Ca: Mg ratio was significantly different between locations, varying from 3.9 to 6.0. Dune soils on the bottoms of the dunes showed lower pH values which can be explained by accumulation of soil organic material (debris of coniferous trees, shrubs, accumulation of acid humus) (Sewerniak & Jankowski, 2017; Sewerniak *et al*., 2017). Nutrient limitation and nutrient availability affect the competition between different species and the species composition of plant communities (Chapin *et al*., 1986; Koerselman & Meuleman, 1996).

According to ordination analysis, bryophyte and lichen species composition on fixed *P. sylvestris* dominated dunes was most significantly determined by aspect, vascular plant species cover, amount of photosynthetically active radiation, thickness of the O_e sub-horizon and soil volumetric water content, acidity and electrical conductivity. As observed by Sewerniak *et al*. (2017), on dune areas topography plays an important role in soil development, thereby affecting the variability and distribution of vegetation. Our results confirmed this statement as far as epigeic bryophytes and lichens were concerned. As to an earlier finding by Sewerniak (2016), the height and slope aspect play an important role in determining the light and moisture regime on dune forests, our results confirmed the importance of the slope aspect in modifying the soil moisture regime on sites with different cardinal directions.

Zonal variation of ground vegetation is considered typical for dunes, although it has been described mostly for vascular plant species (Lane *et al*., 2008; Tilk *et al*., 2017). The study on Rannametsa dunes showed that the species richness of bryophytes and lichens varied along the dune profile. According to our results, bryophytes preferred lower and moister bottoms of the dunes where their species richness was the highest. In addition, the species composition of bryophytes on the bottoms differed significantly from the species composition of the slopes and tops, according to the results of MRPP tests. This can be explained by more humid soils on the bottoms of the dunes. Higher moisture availability on dunes raises plant-specific diversity and the number of plant groups increases (Latorre *et al*., 2013). Soil moisture is important to moss species composition (Proctor, 2008), and fine-scale differences in soil moisture probably have a major effect on the bryophyte community (Grytnes *et al*., 2006). Analysis of indicator species also pointed out *Brachythecium erythrorrhizon* and *B. oedipodium* (species preferring moist habitats according to Düll (1991)) as indicator species for dune bottoms.

At the same time, the lichen species richness was the highest on the slopes of the dunes where patches without vascular plants occurred and bryophyte species were not dominated. In stable and stress-free areas, slow-growing lichens are usually crowded out by vascular plants and by the more vigorous bryophytes because of lichens inability to cope with shading by shrubs or tree canopies, accumulation of humus and leaf litter or substrate instability (Hale, 1974). According to our results, the composition of bryophyte and lichen species was affected by the cover of vascular plant species; similar results were registered by Pharo *et al*. (1999), who found that the cover of vascular plants explains significant variations in fern, bryophyte and lichen species richness.

The light radiation is another key factor determining the diversity and composition of terrestrial lichens (Palmquist, 2000; Márialigeti *et al.,* 2016) because lichens require sufficient light for photosynthesis and growth, while mosses are able to efficiently take advantage of the low irradiances in the shade of the tree canopies (Kolari *et al.*, 2006). Terrestrial lichens are probably limited by light availability rather than soil moisture (Palmquist, 2000). Based on our results, certain lichens (species of *Cladonia*) seem to prefer open dune areas, where PAR is high and soil moisture is low. The proportion of light-demanding species was high among lichen species (the most frequent values of light indices 6—8). Bryophyte species showed more variable light preferences (the values of light indices varied between 3 and 9) and both shade-demanding and full-light requiring bryophyte species were represented on dunes.

Acidity preference of bryophyte species was also variable, ranging on a scale from acid to weakly acid/weakly neutral. Although bryophytes receive nutrients mainly from precipitation (including leachates from tree canopies and plant leaves) (Oechel & Van Cleve, 1986), the nutrient properties and pH of the substrate can also be important and affect bryophyte and lichen species composition (Pausas, 1994). Ketner-Oostra & Sykora (2000) found that when carbon content and acidity increase, the vegetation will change from lichen-poor to moss-rich communities. The number of moss species is more limited by soil moisture than by soil nutrients and a positive relationship for the pH was found by Pausas (1994). Based on NMDS ordination it can be concluded that lichen and bryophyte species composition was dependent on the soil pH, although a previous work compiled in the dune area in south-west Estonia (Kösta & Tilk, 2008) found no influence of the soil pH on the distribution of bryophyte and lichen species.

In addition, a previous study (Sun *et al*., 2013) indicates that bryophyte distribution depends on the depth of litter. Our results agree with this statement, as the bryophyte and lichen species composition was affected by the thickness of the moderately decomposed organic layer. Magnusson (1982) found that certain lichens (species of *Cladonia*) colonise coastal dune areas in southern Sweden where litter has accumulated. Considering future research, we suggest that lichens and bryophytes should be separately analysed because of their different responses to environmental factors.

Conclusions

Altogether 30 species of bryophytes and 22 species of lichens were found on the study area. The average lichen species richness was the highest on the slopes of the dunes, while the highest average bryophyte species richness occurred on the bottoms of the dunes. The highest number of lichen species was identified as light-demanding while the light preference of bryophyte species was more variable. The distribution of bryophyte and lichen species between zones showed significant differences, and therefore it can be concluded that zonation of bryophyte and lichen species can be found on dunes just as it has been described for vascular plant species. In conclusion, it can be said that factors affecting the bryophyte and lichen species composition are related to the dune slope effect, which causes differentiation of soils and therefore a complex of different microhabitats populated by different species. According to our results, some of the most important factors are the aspect of the dune, vascular plant species cover, light conditions, a thickness of the medium decomposed soil organic horizon and soil pH, electrical conductivity and volumetric water content.

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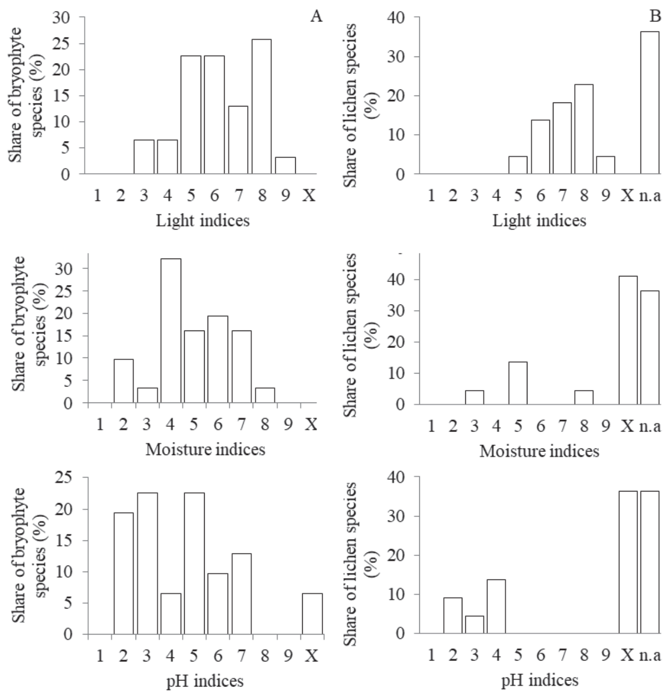

Figure S1. Distribution of (A) bryophyte and (B) lichen species in groups according to ecological indicator values, X indicates the share of species with broad amplitude and n.a shows the share of species where information about indices is not available.

Supplementary figure to the article "Effect of environmental factors on the composition of terrestrial bryophyte and lichen species in Scots pine forests on fixed sand dunes", by Mari Tilk, Katri Ots and Tea Tullus. Forest Systems Vol. 27 No. 3, December 2018 (https://doi.org/10.5424/fs/2018273-13488)

Table S1. Species distribution in different locations.

Location on dune	No. of species in common	Species
Bottom Slope Top	9	*Dicranum polysetum, Brachythecium starkei, Eurhynchium pulchellum, Ptilium crista-castrensis, Cladonia chlorophaea, Pleurozium schreberi, Hylocomium splendens, Dicranum scoparium, Dicranum bonjeanii*;
Bottom Top	1	*Ptilidium ciliare*;
Slope Top	4	*Cladonia stellaris, Cladonia ciliata, Cladonia arbuscula, Cladonia squamosa*;
Bottom Slope	3	*Rhytidiadelphus triquetrus, Cladonia scabriuscula, Brachythecium oedipodium*;
Top	1	*Eurhynchium praelongum;*
Bottom	9	*Eurhynchium angustirete, Brachythecium erythrorrhizon, Plagiomnium medium, Pohlia nutans, Cladonia pyxidata, Drepanocladus aduncus, Cladonia cariosa, Cirriphyllum piliferum, Cladonia coniocraea;*
Slope	26	*Plagiomnium affine, Cephalozia bicuspidata, Cetraria islandica, Dicranum flagellare, Cladonia rei, Cladonia mitis, Cladonia portentosa, Plagiothecium laetum, Cladonia fimbriata, Cladonia acuminata, Cladonia stygia, Campylium stellatum, Campylium sommerfeltii, Cephaloziella rubella, Brachythecium albicans, Cladonia rangiformis, Cladonia rangiferina, Cladonia subulata, Cladonia ochrochlora, Lophozia excisa, Aulacomnium palustre var. imbricatum, Dicranum majus, Ceratodon purpureus, Aulacomnium palustre, Cladonia cryptochlorophaea, Cladonia furcata.*

Supplementary table to the article "Effect of environmental factors on the composition of terrestrial bryophyte and lichen species in Scots pine forests on fixed sand dunes", by Mari Tilk, Katri Ots and Tea Tullus. Forest Systems Vol. 27 No. 3, December 2018 (https://doi.org/10.5424/fs/2018273-13488)

IV

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Variability of bryophytes and lichens on a forested coastal dune Tõotusemägi in Southwestern Estonia

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Abstract. Bryophytes and lichens are important in all dry land ecosystems due to their ability to colonize different substrates which are not suitable for vascular plants. They have an important role in vertebrates and invertebrate's food chain and function as a habitat for invertebrates. Nitrogen and carbon cycles in the forest depend greatly on the local bryophyte and lichen flora. The aim of present study was to investigate the frequency and variety of different species of bryophytes and lichens on the forested sand dune Tõotusemägi. The study was carried out on a 183 m long transect running on the western slope of the dune. Identification of bryophyte and lichen species was carried out and zonality of forest ground vegetation was demonstrated. Species were observed on the ground, on litter, on stumps and on trees. On the slope, 26 bryophyte species and 38 lichen species were registered. Dominating bryophyte species were *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp., *Polytrichum juniperinum* Hedw., *Polytrichum piliferum* Hedw, *Dicranum polysetum* Sw., *Dicranum scoparium* Hedw. Dominating lichen species were *Cladina rangiferina* (L.) Nyl., *Cladina arbuscula* (Wallr.) Hale & W. L. Culb., *Cladonia furcata* (Huds.) Schrad, *Cetraria islandica* (L.) Ach. Dominating species of epiphytic lichens were *Hypogymnia physodes* (l.) Nyl., *Parmelia sulcata* Taylor, *Pseudevernia furfuracea* (L.) Zopf, *Parmeliopsis ambigua* (Wulfen) Nyl. and *Imshaugia aleurites* (Ach.) S. L. F. Meyer. On the slope of the dune 12 different ground vegetation zones were distinguished. Bryophyte species characteristic for humid habitats and tolerant to shade were observed on foot of the dune. This may be caused by a stream flowing nearby which creates a more moist and nutrient rich habitat. The top area of the dune is open to direct UV radiation, therefore lichens and only some bryophyte species tolerant to dryness were observed.

Key words: costal dunes, dune forests, bryophytes, lichens.

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Introduction

Epiphytic bryophytes and lichens are important components of biological diversity in natural boreal and temperate forests (Söderström, 1988; Lesica *et al.*, 1991; Longton, 1992; Esseen *et al.*, 1997). Bryophytes provide a number of important ecological and social uses worldwide, for example, they play a significant role in carbon and nitrogen cycling (Glime, 2001; Turetsky, 2003). The results of Goulden and Crill (1997) showed that the moss-dominated ground vegetation of black spruce forests could account for up to 50% of the total forest photosynthesis. Bryophytes and lichens function as habitat for invertebrates (Suren, 1991) and as seedbeds for forest plants (Glime, 2001). These nonlignified plants influence vegetative successional patterns following disturbance (Jonsson, 1993) and serve as bio-indicators of environmental change (Winner & Bewley, 1978; Gignac, 2001). On dunes bryophytes and lichens can act like pioneer plants; they trap and hold windblown sand in the foredune and help create conditions which encourage the establishment and growth of other plant communities such as woodland, scrub, heath and forest (Jonsson & Esseen, 1990; Andersson & Hytteborn, 1991; Gustafsson *et al.*, 1992; Crites & Dale, 1998; Krys & Jonsson, 1999; Kimmerer, 2005). So far, however, diversity studies only rarely have been carried out on bryophytes (Lee & La Roi, 1979), lichens (Holien, 1997), or both (Wolf, 1993; Mucina *et al.*, 2000; Grytnes *et al.*, 2006).

Dunes represent an extremely complex and fragile habitat type. Vegetation is the key factor in dune stability and it is the vulnerability of dunes vegetation that makes the dunes sensitive to impact (NSW Coastline Management Manual, 1990). Fixed dunes contain important biodiversity both at the species and at the species community level, and they are considered as a priority habitat by the European habitat directive (Council Directive 92/43/EEC).

Maintenance of biodiversity is an integral part of the concept of "sustainable management", but human activity, like tourism and different outdoor activities, often are disturbing the basic equilibria, damaging the fragile vegetation and deteriorating the dune system. Külvik & Tambets (1998) emphasize the importance of dune forests to soil conservation, which in turn allows rare species to retain.

The purpose of this study was to describe and compare the richness of bryophyte and lichen species on a transect from foot to the top of the dune Tõotusemägi. This research should provide a slight insight into how variation of microenvironmental conditions, like soil pH and the location on the transect, influence the distribution of bryophyte and lichen species on the western slope of dune. The results of this research give us new knowledge about bryophytes and lichens diversity on dunes in Rannametsa area and results can be used as practical ecological background information for the elaboration of forest management policy.

Material and Methods

Study area

The study area is located in Luitemaa Nature Reserve (former Rannametsa-Soometsa Nature reserve) in Pärnu County in Southwest Estonia (Figure 1).

Luitemaa nature reserve has been created to protect the dunes formed by Lake Ancylus and Littorina Sea during the ice ages, the ecosystems on the dunes, coastal meadows and also rare and endangered species living in the area (Kiristaja & Timm, 2002).

In Luitemaa, there are two ancient dune chains. One of them is known as Võidu – Soometsa dune chain and the other as Rannametsa dune chain. Between the dunes lays a bog named Tolkuse. Pine stands with *Cladina*, *Vaccinium* and *Calluna* site types are dominant on Rannametsa dunes. The survey was conducted on Tõotusemägi, one of the highest dunes in Rannamtesa dune landscape. It is situated nearby Tallinn-Riga highway.

Fieldwork

Fieldwork was done in four days: June 19-20, 2004, October 10, 2004 and April 24, 2005. The 183 meters long transect runs on the western slope of Tõotusemägi. It

Figure 1. Location of the research area.
Joonis 1. Uurimisala paiknemine.

begins from the foot and reaches to the top of the dune. Transect begins about 6 meters from the stream flowing on the foot of the dune.

Bryophyte and lichen species were observed one meter to both sides of the transect from foot to top of the dune. On the study area samples of bryophytes and lichens were collected from different substrates: from the ground, from tree-trunks, from stumps and from litter and used for further identification of species. Zonality of forest ground vegetation was determined visually according to species variation. The survey was conducted simultaneously with general botanical analysis (Mandre *et al.*, 2006) and the zones were named after dominating vascular plant.

Bryophytes and lichens have no roots and only upper layer of the soil influences their functioning. In each zone, three randomly chosen sample points were established and soil samples from upper 2 cm layer (litter layer) were taken for pH analyses.

Laboratory work and data analysis

More than 200 individuals of bryophytes and lichens were collected from Tõotusemägi. The samples are preserved in the herbarium of Tallinn Botanic Garden. The species were identified in Tallinn Botanic Garden and Tallinn University by using dissecting and compound light microscopes.

For identification of bryophyte and lichen species three different manuals were used (Trass & Randlane, 1994; Ingerpuu & Vellak, 1998; Randlane & Saag, 2004)

For the identification of lichens, 3 different reagents were used:

1) 10% KOH hydrosol
2) $Na(ClO)_2$ saturated hydrosol
3) 5% $C_6H_4(NH_2)_2$ alcoholic solution

Using the reagents on the cortex, on the medulla or on the apothecia of lichen thallus evokes color reactions which expose the existence or the absence of different lichen substances (pigments, toxins) in the individuals being identified.

The pH of collected soil samples was measured in the laboratory of Estonian University of Life Sciences, Forest research Institute, Department of Ecophysiology. Soil pH was measured (n = 5 per sample) in a soil-water suspension (1:5) using a laboratory pH-meter (Mettler Toledo MP220). Regression analysis was made to find a correlation between relative height and soil pH of the sampling site.

Correlations between number of different bryophyte and lichen species and the zones were calculated using correlation matrices. The normality of variables was checked by Lilliefors and Shapiro-Wilks tests. To normalize the variables the log-transformation was used. For correlations, software Statistica 7,0 was used, significance level a = 0,05 was accepted in all cases.

Results

Altogether 26 species of bryophytes and 38 species of lichens were registered on Tõotusemägi (Appendix 1). A clear zonality of forest ground vegetation was observed and 12 different zones of bryophytes and lichens were distinguished on the transect (Figure 2). The zones were named after dominating vascular plant species.

The number of registered bryophyte and lichen species varied between the zones. Correlation analyses revealed dependence between the number of lichen species and relative height of the zones (r = 0,63; p = 0,028), the number of lichen species increases in correlation to the height growth. Correlation showed no statistically reliable dependence between the number of bryophyte species and zones, therefore the bryophyte species richness seems not to be related to the relative height of the zone.

The soil pH was measured in each zone and regression analysis was made, but no significant dependence between the location of the sampling site and pH was found for the upper layers of soil (R^2 = 0.432).

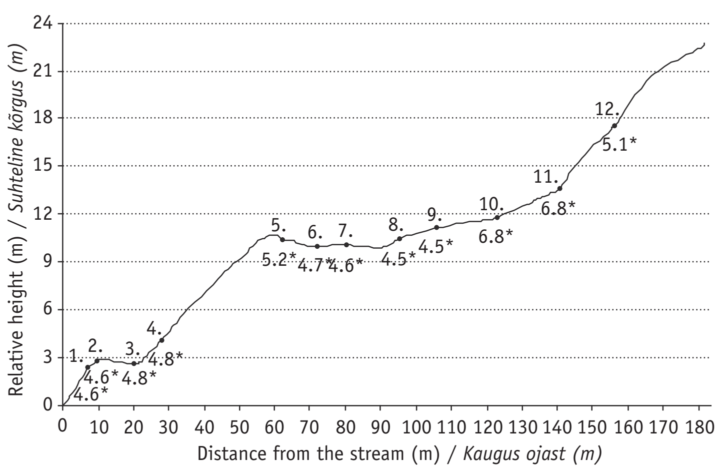


Figure 2. Zonality of bryophytes and lichens on western slope of dune Tõotusemägi. Zero point indicates the location of the stream on the foot of the dune. The number indicates the beginning of different bryophyte and lichen zones; * – the number shows mean value of soil pH in different bryophyte and lichen zones on the depth of 2 cm.

*Joonis 2. Sammalde ja samblike vööndilisus Tõotusemäe läänenõlval. Nullpunkt tähistab oja asukohta luite jalamil. Number tähistab erinevate sambla- ja samblikuvööndite algust; * – number tähistab kuni 2 cm sügavuse pinnasekihi pH keskmist väärtust erinevates sambla- ja samblikuvööndites.*

Dominating bryophyte species on the slope were *Hylocomium splendens* (Hedw.) Schimp. and *Pleurozium schreberi* (Brid.) Mitt. – registered in 6 zones, *Dicranum polysetum* Sw. and *Dicranum scoparium* Hedw. – registered in 4 zones. Dominating lichen species on the slope were *Cladina rangiferina* (L.) Nyl. – registered in 5 zones, *Cladina arbuscula* (Wallr.) Hale & W. L. Culb. and *Cladonia furcata* (Huds.) Schrad – registered in 4 zones, *Cetraria islandica* (L.) Ach. – registered in 3 zones. *Hypogymnia physodes* (L.) Nyl. – registered in 4 zones, *Parmelia sulcata* Taylor and *Pseudevernia furfuracea* (L.) Zopf – registered in 3 zones, *Imshaugia aleurites* (Ach.) S. L. F. Meyer and *Parmeliopsis ambigua* (Wulfen) Nyl. – registered in 3 zones, were the dominating species of epiphytic lichens registered.

Some bryophyte species (*Amblystegium serpens* (Hedw.) Schimp., *Aulacomnium palustre* (Hedw.) Schwaegr., *Bryum flaccidum* Brid., *Cephalosiella hampeana* (Nees) Schiffn., *Herzogiella seligeri* (Brid.) Iwats., *Lophocolea heterophylla* (Schrad.) Dum., *Plagiomnium cuspidatum* (Hedw.) T. Kop.) and some lichen species (*Cladina ciliata* (Stirt.) Trass, *Cladina tenuis* (Flörke) Ahti & M. J. Lai, *Cladonia phyllophora* Hoffm.) were registered only in 1 zone on the transect.

On the foot of the dune there was a stream. The ground was more humid and shady and more species of bryophytes were represented there than on the top area of the dune. Some of these species like *Aulacomnium palustre* (Hedw.) Schwaegr., *Eurhynchium praelongum* (Hedw.) Schimp., *H. seligeri*, *Rhytidiadelphus triquetrus* (Hedw.) Warnst., *P. cuspidatum*, *Plagiomnium undulatum* (Hedw.) T. Kop. and individuals of *Brachythecium* spp. were characteristic only to humid habitats. There were fewer trees on the top area of the dune than on the foot of the dune and the sites were more open to direct UV-radiation. The sites on the top area of the dune also endured under human influence. Mostly lichens (individuals of *Cetraria* spp., *Cladina* spp. and *Cladonia* spp.) and only some species of bryophytes that bear dryness and treading like *B. flaccidum*, *Pohlia nutans* (Hedw.) Lindb., *Polytrichum juniperinum* Hedw., *Polytrichum piliferum* Hedw. and *Racomitrium canescens* (Hedw.) Brid. were registered on these sites (Figure 3).

Zone 1. *Pteridium aquilinum*

The zone began 6 meters from the stream. Habitat was humid and the coverage of vascular plants was dense. Bryophyte species characteristic to humid habitats were registered. Mostly the individuals of *Brachytecium* spp., *Plagiotecium* spp., *R. triquetrus*, *P. undulatum*, *P. cuspidatum* were observed on the site. *A. serpens* was not registered on any other site on the transect.

No lichens were registered on the ground. The individuals of epiphytic lichens *Lecanora* spp. and *Loxospora elatina* were registered on the trunks of *Alnus incana*.

Zone 2. *Deschampsia flexuosa – Calamagostis arundinacea*

Dense coverage of vascular plants left a little room for bryophytes. Most of the species registered in this zone were the same as in Zone 1. The individuals of two species: *L. heterophylla* and *B. flaccidium* were not observed on any other site on the slope.

Zone 3. *Convallaria majalis*

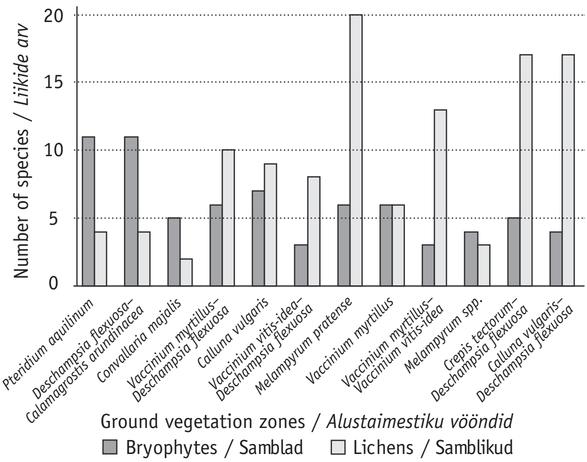
Forest canopy was denser here. Coverage of bryophytes was dense, registered species were characteristic to humid habitats and tolerant to shade. Dominant species were *H. splendens*. Epiphytic individuals of *Lecanora* spp. and *Chaenotheca* spp. were registered on the trunks of *Pinus sylvestris*.

Zone 4. *Vaccinium myrtillus – Deschampsia flexuosa*

The coverage of bryophytes was dense. Dominating species were *H. splendens* and *P. schreberi*. Some assemblages of *D. polysetum* and *D. scoparium* were observed.

The individuals of epiphytic lichen species *Lepraria incana* (L.) Ach., *H. physodes*,

Figure 3. Number of bryophyte and lichen species in different forest ground vegetation zones.
Joonis 3. Sambla- ja samblikuliikide arvukus erinevates alustaimestiku vööndites.



P. furfuracea, *I. aleurites*, *P. sulcata* and *P. ambigua* were registered on *P. sylvestris*.

Zone 5. *Calluna vulgaris*

This zone was situated on a plateau, a plainer area on the slope. Forest canopy was sparse and the site was open to direct UV radiation. Bryophyte individuals which bear dryness were registered on the site: *Ceratodon purpureus* (Hedw.) Brid., *P. piliferum*, *P. nutans* and *D. scoparium*. The coverage of lichens was dense and the individuals of *C. arbuscula*, *C. rangiferina*, *Cladonia chlorophaea* (Flörke ex Sommerf.) Spreng., *Cladonia coniocraea* (Flörke) Spreng., *Cladonia cornuta* (L.) Hoffm., *Cladonia crispata* (Ach.) Flot., *C. furcata*, *Cladonia merochlorophaea* Asahina were registered.

Zone 6. *Vaccinium vitis-idea – Deschampsia flexuosa*

Forest canopy was denser here than described in Zone 5. Dominating species of bryophytes registered in the zone were *P. schreberi*, *D. polysetum* and *D. scoparium*. The coverage of lichens was much less dense compared to Zone 5. In addition to the species characterized in Zone 5, individuals of *Cladonia botrytes* (K. G. Hagen) Willd. and *Cladonia digitata* (L.) Hoffm. were registered. Individuals of epiphytic *H. physodes* were registered on the trunks of *P. sylvestris*.

Zone 7. *Melampyrum pratense*

Bryophyte species registered in this zone were the same as described in Zone 6. The coverage of lichens was sparse but numerous species were registered on different substrates. *Cladonia cenotea* (Ach.) Schaer., *C. phyllophora, Cladina mitis* (Sandst.) Hustich, *C. ciliata, C. islandica* and *Cetraria aculeata* (Schreb.) Fr. were observed in addition to the lichen species characterized in Zone 5 and Zone 6.

Zone 8. *Vaccinium myrtillus*

The coverage of bryophytes was dense and the dominating species registered were *H. splendens* and *P. schreberi*. An interesting finding was *Aulacomnium palustre* (Hedw.) Schwaegr., which is characteristic to more humid habitats. Some individuals of *Cladonia* spp. and *Cladina* spp. were observed.

Individuals of epiphytic *H. physodes* and *P. furfuracea* were registered on the trunks and branches of *P. sylvestris*.

Zone 9. *Vaccinium myrtillus – Vaccinium vitis-idea*

This zone was similar to Zone 8. Density of bryophytes was high. *P. schreberi*, *D. polysetum* and *D. scoparium* were the dominant bryophyte species in the zone. Lichen species registered were the same as characterized in Zone 8.

Zone 10. *Melampyrum* spp.

The coverage of bryophytes was dense. *H. splendens* and *P. schreberi* were the dominant bryophyte species. Individuals of *C. islandica*, *C. aculeata* were observed.

Zone 11. *Crepis tectorum – Deschampsia flexuosa*

This zone was situated on the last raise of the slope, near to the top of the dune. The forest canopy was sparse and the site was open to direct UV radiation. Some individuals of heat tolerant bryophytes were registered: *C. purpureus*, *P. nutans*, *D. polysetum*, *P. piliferum*. An individual of *Cephalosiella hampeana* (Nees) Schiffn. was documented.

The density of lichens coverage is high. Numerous species of *Cladonia* spp. and some species of *Cladina* spp. and *Cetraria* spp. were registered.

Zone 12. *Calluna vulgaris – Deschampsia flexuosa*

The zone was situated on the top area of the dune where the forest canopy is almost non-existent. Only some individuals of bryophytes were registered. The density of lichens coverage was high. The bryophyte and lichen species were the same as characterized in Zone 11.

Discussion and Conclusions

The age of dune and climatic conditions play an essential role in the formation of dune ecosystems, but the most important factor influencing the flora and the habitats of bryophytes and lichens on the slope of the dune is the structure of surrounding forest canopy. It creates a special microclimate for the sites and the individuals colonizing them. (Sulima & Coxon, 2001) The results of this research proved the occurrence of variety of site types and zonality along the slope. This may be caused by different topographic and edaphic conditions in the study area. The pH seems not to influence the distribution of bryophyte and lichen species. The height growth influences the distribution of lichen species, but does not seem to have an influence on bryophytes. Some of the zones were relatively narrow which may be caused by narrow changes in the structure of forest canopy affecting the amount of UV radiation reaching the forest ground and water runoff.

The results, received from the survey, could be used for geobotanical studies of comparison and for characterization of the structure of analogous dune forests as ecosystems.

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Appendix 1. Bryophytes and lichens registered on Tõotusemägi.
Lisa 1. *Tõotusemäel registreeritud samblikud ja samblad.*

Family / *Sugukond*	Species / *Liik*	Locality* / *Koht**
Lichens / *Samblikud*		
Arthoniaceae	*Arthonia radiata* (Pers.) Ach.	4
Cladoniaceae	*Cladina arbuscula* (Wallr.) Hale & W. L. Culb.	5-7; 9
	Cladina ciliata (Stirt.) Trass	7
	Cladina mitis (Sandst.) Hustich	7; 9; 11; 12
	Cladina portentosa (Dufour) Follmann	9
	Cladina rangiferina (L.) Nyl.	5-9
	Cladina tenuis (Flörke) Ahti & M. J. Lai	7
	Cladonia botrytes (K. G. Hagen) Willd.	6
	Cladonia cenotea (Ach.) Schaer.	7; 11; 12
	Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.	5-7
	Cladonia coniocraea (Flörke) Spreng.	1; 5; 7; 9; 11; 12
	Cladonia cornuta (L.) Hoffm.	5; 7-9
	Cladonia crispata (Ach.) Flot.	5-7; 9; 11; 12
	Cladonia digitata (L.) Hoffm.	6; 9
	Cladonia fimbriata (L.) Fr.	11
	Cladonia floerkeana (Fr.) Sommerf.	11; 12
	Cladonia furcata (Huds.) Schrad	5-12
	Cladonia gracilis (turbinata) (Ach.) Ahti	7-9; 11; 12
	Cladonia merochlorophaea Asahina	5; 7; 11; 12
	Cladonia phyllophora Hoffm.	7
	Cladonia pyxidata (L.) Hoffm.	11; 12
Coniocybaceae	*Chaenotheca ferruginea* (Turner & Borrer) Mig.	2, 3
Lecanoraceae	*Lecanora carpinea* (L.) Vain.	1-3
	Lecanora expallens Ach.	3; 11, 12
	Lecanora pulicaris (Pers.) Ach.	1-3
	Lecidella elaeochroma (Ach.) M. Choisy	1
Lecideaceae	*Hypocenomyce anthracophila* (Nyl.) P. James & Gotth. Schneid.	11; 12
	Hypocenomyce scalaris (Ach.) M. Choisy	11; 12
Loxosporaceae	*Loxospora elatina* (Ach.) A. Massal.	4
Parmeliaceae	*Cetraria aculeata* (Schreb.) Fr.	7; 10-12
	Cetraria islandica (L.) Ach.	7; 9-12
	Hypogymnia physodes (L.) Nyl.	4; 6-9
	Imshaugia aleurites (Ach.) S. L. F. Meyer	4
	Parmelia sulcata Taylor	4
	Parmeliopsis ambigua (Wulfen) Nyl.	4; 7; 11; 12
	Pseudevernia furfuracea (L.) Zopf	4; 7-9
	Usnea hirta (L.) F. H. Wigg.	4; 11
Stereocaulaceae	*Lepraria incana* (L.) Ach.	2; 4; 7; 11; 12
Bryophytes / *Samblad*		
Amblystegiaceae	*Amblystegium serpens* (Hedw.) Schimp.	1
Aulacomniaceae	*Aulacomnium palustre* (Hedw.) Schwaegr.	1; 8
Brachytheciaceae	*Brachythecium albicans* (Hedw.) Schimp.	1; 3; 7
	Brachythecium oedipodium (Mitt.) Jaeg.	1-4; 7
	Brachythecium salebrosum (F.Web. & Mohr.) Schimp.	1; 3; 7
	Brachythecium velutinum (Hedw.) Schimp.	1-4; 7; 8
	Eurhynchium praelongum (Hedw.) Schimp.	2
Bryaceae	*Bryum flaccidum* Brid.	2
Cephaloziellaceae	*Cephaloziella hampeana* (Nees) Schiffn.	11
Dicranaceae	*Dicranum polysetum* Sw.	2-10
	Dicranum scoparium Hedw.	1-12
Ditrichaceae	*Ceratodon purpureus* (Hedw.) Brid	5; 11; 12
Geocalycaceae	*Lophocolea heterophylla* (Schrad.) Dum.	2
Grimmiaceae	*Racomitrium canescens* (Hedw.) Brid.	11
Hylocomiaceae	*Hylocomium splendens* (Hedw.) Schimp.	3; 4; 7; 10
	Pleurozium schreberi (Brid.) Mitt.	2; 4-10
	Rhytidiadelphus triquetrus (Hedw.) Warnst.	1
Hypnaceae	*Herzogiella seligeri* (Brid.) Iwats.	1
Hypnaceae	*Hypnium cupressiforme* Hedw.	1; 2

Family / *Sugukond*	Species / *Liik*	Locality* / *Koht**
Mielichhoferiaceae	*Pohlia nutans* (Hedw.) Lindb.	5; 11; 12
Plagiomniaceae	*Plagiomnium cuspidatum* (Hedw.) T.Kop.	1
	Plagiomnium undulatum (Hedw.) T.Kop.	1
Plagiotheciaceae	*Plagiothecium laetum* Schimp.	2; 3; 7
Polytrichaceae	*Polytrichum juniperinum* Hedw.	5
	Polytrichum piliferum Hedw.	2; 11; 12
Pottiaceae	*Tortula ruralis* (Hedw.) Gaertn. Et al.	12

* Indicates species locality on the transect, number of zones.
* *Näitab liigi paiknevust transektil, vööndi numbrit.*

Sammalde ja samblike varieeruvus Edela-Eesti luidetel Tõotusemäe näitel

Helen Kösta ja Mari Tilk

Kokkuvõte

Töö eesmärgiks oli selgitada erinevate sambla- ja samblikuliikide esinevused ning liigilise koosseisu varieeruvus Rannametsa luitestiku ühel kõrgeimal luitel – Tõotusemäel. Uuritava transekti kogupikkus oli 183 m, see paiknes luite läänenõlval. Transektil määrati erinevad sambla- ja samblikuliigid ning alustaimestu tsonaalsus. Erinevatest pinnasekihtidest võeti analüüse pH määramiseks.

Kihtides sügavusega kuni 2 cm statistilist sõltuvust prooviruudu suhtelise kõrguse ja mulla ülemiste kihtide pH vahel ei täheldatud, seega sammalde ja samblike vööndilisus nõlval ei olnud nähtavasti tingitud mulla pealmiste kihtide pH väärtusest.

Kokku registreeriti transektilt 26 samblaliiki ning 38 samblikuliiki. Sammaldest domineerisid harilik palusammal (*Pleurozium schreberi* (Brid.) Mitt.), harilik laanik (*Hylocomium splendens* (Hedw.) Schimp.) ning harilik (*Dicranum scoparium* Hedw.) ja lainjas kaksikhammas (*Dicranum polysetum* Sw.).

Domineerivad samblikuliigid olid harilik põdrasamblik (*Cladina rangiferina* (L.) Nyl.), mets-põdrasamblik (*Cladina arbuscula* (Wallr.) Hale & W. L. Culb.) ning harkjas porosamblik (*Cladonia furcata* (Huds.) Schrad). Epifüütsetest samblikest esinesid Eestis kõige sagedasemad lehtsamblikud; harilik hallsamblik (*Hypogymnia physodes* (L.) Nyl.) ja vagu-lapiksamblik (*Parmelia sulcata* Taylor), hall karesamblik (*Pseudevernia furfuracea* (L.) Zopf), kollane lagusamblik (*Parmeliopsis ambigua* (Wulfen) Nyl.) ja hall terasamblik (*Imshaugia aleurites* (Ach.) S. L. F. Meyer).

Luite läänenõlval registreeriti kokku 12 erinevat taimestiku vööndit, mida iseloomustavad erinevad valgus- ja niiskustingimused, substraadi iseärasused ning erinevate taimeliikide esinemine. Alumistes vööndites, kus niiskust on rohkem, domineerivad samblad, leidub vaid üksikuid samblikuliike, kõrgemates vööndites, kus puistu liituvus on väiksem, domineerivad kuivust taluvad samblikuliigid.

Registreeritud sambla- ja samblikuliigid olid enamjaolt luitemetsadele iseloomulikud, nende esinemine alal oli oodatav.

Saadud tulemusi võiks teatud määral üldistada ka teiste samalaadsete luidete kohta, kasutada geobotaanilistes võrdlusuuringutes ning luitemetsade kui ökosüsteemide struktuuri iseloomustamisel.

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2005 – 2008 Estonian Science Foundation grant. "Role of carbohydrate metabolism in the adaptation of trees to the variety of nutritional environment (ETF6026)". Principal Investigator.

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2008 – 2009 SA Keskkonnainvesteeringute Keskus. „Noorte puistute kasv ja biomass ammendatud põlevkivikarjääri puistangutel (8-2/T8158MIMI)“. Põhitäitja.

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2005 – 2008 Sihtasutus Eesti Teadusfond. „Süsivesikute ainevahetuse osa puude kohanemisel toitumiskeskkonna mitmekesisusega (ETF6026)“. Põhitäitja.

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